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Abstract approved:

Daniel D. Roby

The Kittlitz's murrelet (*Brachyramphus brevirostris*) is a rare member of the seabird family Alcidae that breeds in coastal areas of Alaska and Beringian Russia. The species belongs to the genus *Brachyramphus,* an unusual seabird taxon in which all three extant species nest non-colonially, situating their nests up to 75 km inland from coastal marine waters. This nesting strategy is different from that of most seabird species, which tend to nest colonially on remote islands or sea cliffs, where terrestrial predators are generally absent or cannot easily access nests. Within the genus *Brachyramphus,* Kittlitz's murrelet is notable because a majority of the global population appears to nest on the surface of the ground in rocky alpine habitat near inland or tidewater glaciers, foraging in adjacent marine waters influenced by glacial outflows. The unusual nesting habits of Kittlitz's murrelet have made the study of its nesting ecology difficult, and gaps therefore exist in our understanding of the species' breeding biology. Kittlitz's murrelet populations have declined substantially in core areas of its range, causing the U. S. Fish

and Wildlife Service to designate the species as a candidate for protection under the Endangered Species Act. A better understanding of Kittlitz's murrelet nesting ecology is crucial for determining potential causes of these declines and for future management of the species. To this end, I studied Kittlitz's murrelet breeding ecology and nest site selection during 2008-2011 on Kodiak Island, Alaska, in an unglaciated area that was recently found to have large numbers of accessible nests.

I and my colleagues found 53 active Kittlitz's murrelet nests in inland scree-dominated habitats and placed remote, motion-sensing cameras at 33 nests. Adults exchanged incubation duties at the nest every 24 or 48 h, almost exclusively during early morning twilight. Following hatching of eggs, parents provisioned their single nestling with an average of 3.9 to 4.8 fish per day, depending on the year. Parental visits to the nest during chick-rearing occurred primarily after sunrise in the early to mid-morning hours, and during evening twilight. Fish were delivered singly to the chick, and Pacific sand lance (*Ammodytes hexapterus*), a high-lipid forage fish, accounted for about 92% of all identifiable chick meal deliveries. Chick growth rates were high relative to confamilial species, consistent with the high quality of chick diets; the logistic growth rate constant (K) was 0.291, greater than that for any other semi-precocial alcid. Chicks fledged an average of 24.8 d after hatching and asymptotic chick body mass averaged about 135.5 g, approximately 58% of adult body mass. Age at fledging, asymptotic chick body mass (% adult mass), and the number of meal deliveries required to fledge a chick were all lower than or as low as any other species of semi-precocial alcid.

The average estimated nest survival rate during 2008-2011 was 0.093 (95% CI = 0.01–0.30), which is extremely low compared to other species in the family Alcidae, and is almost certainly insufficient to sustain a stable population. The primary causes of nest failure were depredation (47% of total nest fates), mostly by red foxes (*Vulpes vulpes*), and unexplained nestling mortality on the nest (21% of nest fates). Saxitoxin and/or pathogenic endoparasite burdens were observed in five of six necropsied chick carcasses, suggesting possible causes for chick mortality not directly attributable to predation.

Habitat characteristics of Kittlitz's murrelet nest sites differed significantly from unused sites at several scales. At a small scale (within 5 m of the nest), nest sites had a lower percent coverage of vegetation and higher percent coverage of intermediate-sized rocks (5–30 cm diameter), compared to randomly selected unused sites. Nest sites were also located on steeper, more north-facing slopes compared to randomly selected sites. Nest sites also had a lower percent coverage of vegetation than randomly-selected sites at larger scales (within 25 m and 50 m of the nest site). Nest sites were located significantly farther from the edge of densely-vegetated habitats than random sites. There was no evidence that nest sites were different from randomly-selected sites in terms of elevation, proximity to ridgelines, or proximity to the open ocean, although a low degree of variation within the study area for these habitat characteristics may have precluded detection of potential differences. Nest survival rates did not co-vary with slope, percent vegetation coverage, distance from vegetated edges, or percent cover of intermediate-sized rocks; however, this result may be an artifact of a limited sample size.

The results of this thesis will provide managers with a better understanding of the factors that may limit Kittlitz's murrelet nesting success, such as nest predation and forage fish availability, as well as factors that may influence the quality and distribution of Kittlitz's murrelet nesting habitat in the future, given on-going and progressive climate change.

Breeding Ecology and Nest Site Selection of Kittlitz's Murrelets on Kodiak Island, Alaska

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I understand that my thesis will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my thesis to any reader upon request.

Matthew James Lawonn, Author

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TABLE OF CONTENTS

TABLE OF CONTENTS (continued)

Page

LIST OF FIGURES

LIST OF FIGURES (Continued)

LIST OF TABLES

LIST OF TABLES (Continued)

BREEDING ECOLOGY AND NEST SITE SELECTION OF KITTLITZ'S MURRELETS ON KODIAK ISLAND, ALASKA

CHAPTER 1

GENERAL INTRODUCTION

Matthew James Lawonn

Kittlitz's murrelet (*Brachyramphus brevirostris*) is a rare Beringian seabird within the family Alcidae. Its breeding range extends throughout much of coastal Alaska, where an estimated 70% of the global population of 30,900 to 56,800 individuals is thought to nest, with the balance breeding in portions of eastern Russia (USFWS 2010). Aggregations of Kittlitz's murrelets during the breeding season are patchily distributed and small in size (100–4,500 individuals; van Vliet 1993), and generally occur in areas characterized by glacially influenced marine waters (Kendall & Agler 1998; Day et al. 1999). The species is a member of the genus *Brachyramphus*, which it shares with the marbled murrelet (*B. marmoratus*) and long-billed murrelet (*B. perdix*; Friesen et al. 1996). Unlike all other members of the Alcidae, and the overwhelming majority of seabirds in other taxa, *Brachyramphus* species have cryptically-colored breeding plumage and nest non-colonially, generally inland on mainland areas or large islands where terrestrial predators are present (Nelson & Hamer 1995; Gaston & Jones 1998). These traits suggest that *Brachyramphus* murrelets have evolved within the context of elevated predation pressure compared to other alcids (Gaston & Jones 1998). Within *Brachyramphus*, Kittlitz's murrelet is unique in that its nests have generally been found on the surface of alpine scree and talus slopes (Day et al. 1999), rather than on cliffs or in large trees like most nests of marbled and long-billed murrelets (Nelson 1997; Gaston & Jones 1998; Barbaree 2011). Most concentrations of adult Kittlitz's murrelets during the breeding season are located in close proximity to glacially influenced alpine habitats, suggesting the importance of such habitats for nesting (Day et al. 1999; Piatt et al. 1999).

Significant Kittlitz's murrelet population declines have been observed or suggested in many surveyed areas of Alaska within the last 25 years (Kissling et al. 2011; Kuletz et al. 2011a, 2011b; Piatt et al. 2011; USFWS 2011), and in 2004 the U.S. Fish and Wildlife Service (USFWS) named the species as a candidate for protection under the Endangered Species Act. The causes of observed declines in some Kittlitz's murrelet populations, however, are not well understood. The literature has identified sources of mortality and causes of lower productivity, including gill net by-catch, oil spills, and disturbance from vessel traffic (Wynne et al. 1992; van Vliet & McAllister 1994; Agness et al. 2008), but these potential factors in population declines are not evenly distributed across local populations, and thus may not explain the species' apparent widespread decline. Other factors that could conceivably act across a sufficiently large geographical scale include climate-driven changes in marine food webs (Piatt & Anderson 1996; Agler et al. 1999; Anderson & Piatt 1999), decreases in the quality of foraging habitats or efficiency of prey capture due to glacial recession (Kuletz et al. 2003), loss of nesting habitat due to glacial recession and accompanying primary plant succession (USFWS 2011), habitat changes in the overwintering range (Mueter & Litzow 2008), effects of environmental contaminants (USFWS 2011), and changes in the number and distribution of predators of Kittlitz's murrelets (USFWS 2011).

Although it is not known how these factors might affect the demography of Kittlitz's murrelets, there is scattered but increasing evidence that low reproductive output may be limiting population growth (Day & Nigro 2004; Kaler et al. 2009; Lawonn et al. 2012). The study of factors influencing reproductive success, however, has been

limited by the difficulty of locating and accessing the species' nests in remote alpine habitats. As of 1999, only 19 active nests of the species had been described (Piatt et al. 1999), and very few of these had been studied in any detail (Day et al. 1999). Hence, our knowledge of the breeding ecology and nesting habitat requirements of Kittlitz's murrelets is limited, and hampers attempts to identify reasons for poor reproductive success.

The studies detailed herein describe the species' nesting phenology, general nesting behavior, chick provisioning and growth, nest success, and nest site selection within a study area located ca. 70 km from the nearest glaciated terrain, on Kodiak Island, Alaska. Kittlitz's murrelets have only recently been confirmed to nest on Kodiak Island; the first nest was discovered inadvertently in 2006 (Stenhouse et al. 2008), on lands managed by Kodiak National Wildlife Refuge (KNWR). In 2007, Kittlitz's murrelet vocalizations and flight activity were noted by researchers in a different area of KNWR, located in the southwest portion of the island (Day & Barna 2007, Stenhouse et al. 2008). This latter area was attractive for potential research because of the accessibility of presumed nesting habitat, owing to its relatively low elevation and lack of hazardous terrain compared with other potential nesting areas on Kodiak Island. The studies detailed in this thesis were initiated by KNWR and the U.S. Geological Survey, Alaska Science Center in 2008 to research presumed Kittlitz's murrelet breeding activity in this area. During 2008-2011, I and my colleagues discovered 53 active Kittlitz's murrelet nests in southwest Kodiak Island, markedly increasing the number of known nests for the species,

and allowing for a statistically rigorous study of elements of the species' breeding ecology.

The aim of this thesis is to fill critical data gaps relating to Kittlitz's murrelet breeding ecology and nest site selection to better understand factors that might limit reproductive success. This is one of the most comprehensive studies of Kittlitz's murrelet breeding ecology to date, and the results from this study may serve as a baseline for future comparisons across the species' range. Additionally, this research provides information that can be used by researchers and managers to identify and model nesting habitats in unstudied areas, and may enable future nest discoveries that would facilitate improved understanding of the nesting behavior of this enigmatic species. Furthermore, through use of relatively new nest surveillance technology on a large sample of nests, the results from this thesis research comprise one of the more detailed studies of the breeding ecology of any *Brachyramphus* species, and thus may help improve our understanding of the adaptive significance of the life history traits of all *Brachyramphus* murrelets.

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CHAPTER 2

BREEDING ECOLOGY OF KITTLITZ'S MURRELETS ON KODIAK ISLAND, ALASKA

Matthew James Lawonn, Daniel D. Roby, John F. Piatt, William H. Pyle, and Robin M. Corcoran

ABSTRACT

We studied the breeding ecology of Kittlitz's murrelet (*Brachyramphus brevirostris*) on Kodiak Island, Alaska during 2008-2011 as it pertains to the growth and development of chicks, nesting success, and the reproductive investment of parents. We discovered 53 active nests within inland, scree-dominated habitats and placed surveillance cameras at 33 nests. The period of continuous chick brooding by parents lasted between 24 and 48 h post-hatching. Most parental deliveries of food items to nestlings occurred shortly after sunrise and during dusk, although 30.2% of meal deliveries occurred at other times of the day. Chicks were provisioned with an average of 4.34 fish per day throughout the nestling period. Pacific sand lance (*Ammodytes hexapterus*), a high-lipid schooling forage fish, accounted for about 92% of identified chick meals. Chicks grew rapidly; the logistic growth rate constant (K) was 0.291, the highest rate yet documented among semi-precocial alcids. Chicks fledged an average of 24.8 d post-hatching, when chick body mass had reached a mean asymptote of 135.5 g, or 58% of average adult body mass; average age at fledging and asymptotic chick body mass (% of adult mass) were as low or lower than any other semi-precocial alcid. Nest survival rates were very low (mean = 0.093) compared to other alcids, almost certainly too low to support a stable population. In 68% of nests either the contents were depredated (47%) or the nestling died on the nest prior to fledging (21%). The crepuscular timing of parental nest visits, high nestling growth rates, and short nestling periods are consistent with adaptations to high-risk nest sites. The dietary specialization

of parents for provisioning their young with high-lipid forage fish likely mitigates predation risk by reducing the number of parental provisioning visits required to fledge a chick, while also reducing the energetic investment of parent murrelets.

INTRODUCTION

The Kittlitz's murrelet (*Brachyramphus brevirostris*) is a rare and enigmatic seabird species in the family Alcidae. It shares the genus *Brachyramphus* with the marbled murrelet (*B. marmoratus*) and the long-billed murrelet (*B. perdix*), with which it is sympatric across much of its Beringian range. *Brachyramphus* murrelets are anomalous within the Alcidae in that they are non-colonial nesters, have cryptic breeding plumage, and generally nest inland on mainland areas or large islands, rather than on small islands or sea cliffs inaccessible to terrestrial predators (Gaston & Jones 1998, Day et al. 1999). Within the genus *Brachyramphus*, Kittlitz's murrelet is unique in that all described nests have been situated on the surface of the ground, generally on alpine scree and talus slopes, rather than in large trees where many marbled murrelet and long-billed murrelet nests have been found (Konyukhov & Kitaysky 1995; Nelson 1997; Day et al. 1999). Kittlitz's murrelet nests have been found up to 2,000 m elevation and 75 km inland, similar to extremes for marbled murrelet, usually in very rugged terrain (Day et al. 1983, 1999). High at-sea densities of adult Kittlitz's murrelets during the breeding season are usually found near areas with significant glacial outflow, suggesting that nests are often located in nearby glacially-influenced alpine habitats (Agler et al. 1998; Day et al. 2000; Kuletz et al. 2003).

Data from at-sea surveys suggest unexplained population declines for Kittlitz's murrelet in multiple areas of coastal Alaska within the last 25 years, and there is scattered but increasing evidence that low reproductive output may be a key constraint on

population growth rates (Day & Nigro 2004; Kaler et al. 2009; USFWS 2011). Investigations into the factors potentially influencing reproductive success have been limited, however, by gaps in our knowledge of the species' breeding ecology. Very little has been published on this subject, with the notable exception of Kaler et al. (2009); their study presents data on nesting habitat and chick growth for 12 Kittlitz's murrelet nests on Agattu Island, Alaska, a small, remote island in the western Aleutians with no terrestrial predators.

Species within the Alcidae display a high degree of variation in chick age and body mass (relative to adult mass) when they leave the nest, variation that is unparalleled among other avian families. Chicks of some species leave their nests to go to sea as young as 1-2 d post-hatching and as small as 15% of adult mass (precocial murrelets in the genus *Synthliboramphus*), to as old as 50 or more days post-hatching and as large as 100% of adult mass (certain semi-precocial species). Most alcid species, including *Brachyramphus* murrelets, display a semi-precocial mode of development, where the chick spends an extended period in the nest and completes much of its growth and development from hatchling size to adult size, and leaves the nest capable of powered flight (Sealy 1973). Available information for *Brachyramphus* suggests that nestling periods may be shorter and fledging mass lighter than for most semi-precocial alcids (Nelson 1997, Day et al. 1999, Kaler et al. 2009), which is consistent with expectations for nest sites that experience high time-dependent mortality relative to mortality rates experienced by chicks at sea following fledging (Ydenberg 1989).

The emerging body of knowledge about the breeding behavior, nest success rates, and life histories of *Brachyramphus* murrelets in general, and Kittlitz's murrelet in particular, suggests that their nesting areas are indeed high-risk relative to the ocean environment; this is in contrast to other alcids, which are thought to have relatively "safe" nest sites (Ydenberg 1989).The presence of terrestrial predators that can readily access *Brachyramphus* nest sites and the crypsis characteristic of the genus suggest the importance of predation as a selective force in the evolution of the life history of *Brachyramphus* species; this hypothesis is supported by evidence of high rates of nest depredation in both Kittlitz's and marbled murrelets (Nelson & Hamer 1995b; Kaler et al. 2009), and anecdotal evidence of high adult mortality caused by avian predators near nesting habitats (e.g., Kissling 2007).

We recently discovered habitats on Kodiak Island, Alaska with relatively high densities of accessible Kittlitz's murrelet nests. This discovery allowed us to more thoroughly investigate the breeding ecology of Kittlitz's murrelets than has previously been possible. In this paper we present results from the study of 53 active Kittlitz's murrelet nests that were found over a 4-year period. We describe a number of poorly-known elements of Kittlitz's murrelet breeding ecology, but pay particular attention to aspects of Kittlitz's murrelet breeding ecology that we thought might relate to the suspected "riskiness" of their nest sites compared to non-*Brachyramphus* alcids, including parental attendance, chick diet and growth, and rates of nest survival. We also compare aspects of Kittlitz's murrelet breeding ecology to that of other semi-precocial

alcids to place our findings in an appropriate context, and discuss ways in which Kittlitz's murrelets may be especially sensitive to declines in forage quality compared to other seabirds.

METHODS

Study Area

Kodiak Island lies approximately 50 km southeast of mainland Alaska in the northern Gulf of Alaska, and is by far the largest island in the Kodiak Archipelago, with a land area of 8,975 km^2. Kodiak Island supports a suite of mammalian and avian predators that is similar to areas on mainland Alaska where most of the North American population of Kittlitz's murrelets is presumed to nest. Most of the interior of Kodiak Island consists of mountainous terrain, with a major range extending southwest-northeast along the length of the island; several peaks exceed 1,200 m in elevation. The island's vegetation is dominated by shrub, meadow, and dwarf shrub communities, with approximately 5% of the island's surface consisting of bedrock outcrops and talus/scree slopes, ground cover types known to be used as nesting substrate by Kittlitz's murrelets in other regions of its breeding range (Day et al. 1999).

We studied the breeding ecology of Kittlitz's murrelets in the southwestern portion of the island during 2008-2011. Our overall study area encompassed approximately 700 ha of scree and talus slopes, as well as unbroken bedrock outcrops, at elevations from 80 m to 471 m. Average size of rocks comprising the substrate was

small, with approximately 70% of sampled rock substrate less than 10 cm in diameter. The parent rock material in the study area is classified as ultramafic, a type of igneous rock containing high concentrations of heavy metals and scarce plant nutrients; this combination precludes the growth of most plants (Alexander et al. 2007). Expanses of sparsely vegetated ultramafic scree provide potential Kittlitz's murrelet nesting habitat at relatively low elevations within the study area. Our study was conducted in four areas of contiguous ultramafic scree and outcrops, each exceeding 100 ha in surface area, and each situated from 3 to 6 km from the nearest neighboring area. Our study was concentrated in only one of these four areas during 2008, and expanded to all four areas during 2009-2011. Although Kittlitz's murrelets are often associated with glaciers during the breeding season, the nearest glaciated terrain to the study area was approximately 70 km distant.

We located Kittlitz's murrelet nests by systematically searching slopes dominated by scree, often interspersed with small boulders and bedrock outcrops. Two to five searchers walked 5-10 m apart and abreast of each other, generally following the slope contour from one edge of the scree slope to the other. Following the completion of each search transect, searchers moved perpendicular to the contour and repeated the search transect in the opposite direction until the entire slope had been searched. Areas within 30–50 m of a known active murrelet nest were not searched to avoid disturbance to breeding adults. All but one of the active nests discovered during this study was found when an incubating adult murrelet flushed from its nest; the exception was a nest that was

discovered with an unattended nestling. We identified adult Kittlitz's murrelets upon flushing by their diagnostic white outer rectrices, or upon the adult's return to the nest based on the morphology of the culmen (Day et al. 1999).

Upon discovery of an active nest, we measured egg length and breadth to the nearest 0.1 mm with dial calipers (Mitutoyo 700-126) and weighed eggs to the nearest 0.5 g with a 100-g Pesola LightLine spring scale. We estimated the stage of incubation by floating eggs in a clear container of water, comparing their buoyancy to egg buoyancy benchmarks (Westerskov 1950; Rizzolo & Schmutz 2007) scaled to an assumed incubation period of 30 days (Day et al. 1999). If eggs were pipped when discovered, we assumed that hatching occurred within 1-2 days. Nests were photographed and a small, inconspicuous cairn or indelible ink mark was placed 2-5 m from the nest to facilitate relocation. To minimize the introduction of human scent, we wore latex or nitrile gloves when handling eggs, chicks, or substrate near the nest.

We placed remote still-image, motion-triggered cameras 1–3 m from a subset of active murrelet nests to collect data on nesting behavior, chick provisioning, and nest fate. During 2008 we deployed one camera near a nest containing a chick 12 days after the nest was discovered. During 2009 and 2010, we attempted to deploy cameras on every second nest at the time it was discovered, depending on camera availability. During 2011, we attempted to deploy cameras on every possible active nest at the time of discovery. The following camera types were used during our study: Reconyx Team Primos Silent Image (2008), Reconyx PC90 RapidFire Professional Covert Color IR

(2009-11), and Reconyx PC900 HyperFire Professional High Output Covert Infrared (2010-11). Cameras were painted to blend in with their surroundings prior to deployment, and outfitted with visors to reduce glare reflected from the lens and flash surfaces. We programmed cameras to photograph all motion-triggered events, and most were set to take one photo every three minutes, an interval selected to approximate the minimum time an adult Kittlitz's murrelet remains at its nest while feeding its chick (J. Piatt and N. Naslund, unpubl. data). In 2011, three cameras were programmed to take photos at one-minute intervals to measure with greater precision the length of time for chick provisioning visits and incubation shift exchanges.

We reviewed photos from nest cameras to determine length and timing of incubation shifts, nest depredation events, diet composition, and chick provisioning rates. We assigned fish delivered to chicks to one of the following size classes whenever possible: < 8 cm, 8–12 cm, 12–16 cm, and > 16 cm total length. We used preserved specimens of Pacific sand lance (*Ammodytes hexapterus*; a common forage fish), adult murrelet wing chord length (125–140 mm; Day et al. 1999), and chick total head-bill length (45–55 mm; M. J. Lawonn, unpubl. data) as references for estimating the length of forage fish observed in images. Specimens of discarded forage fish were also collected from the ground near active nests during 2009-2011, and subsequently identified to species. These opportunistic collections corroborated identification of species and size estimates from photographs.

We visited active nests three times during the nestling period to collect data on chick growth rates. We attempted to time our visits to coincide with chick ages of 4–6 days post-hatch, 9–13 days post-hatch, and 19–21 days post-hatch. We weighed chicks using Pesola LightLine spring scales to the nearest 0.5 g (100-g capacity scale) or to the nearest 2.5 g (500-g capacity scale). We measured wing chord to the nearest 1 mm using a flexible metal ruler.

Data Analysis

We analyzed data on chick growth rates using nonlinear mixed effects models from the "nlme" package in the statistical program R (Pinheiro & Bates 2000). Nonlinear mixed effects models account for a lack of independence associated with repeated measurements by considering both individual-specific variation (random effects), and overall population-wide variation (fixed effects; Pinheiro & Bates 2000). We fitted logistic growth curves of the form:

$$y = A/1 + e^{(-K(age-t_i))},$$

where A = asymptotic nestling mass, K = growth rate constant, and t_i = age (days post-hatch) at the inflection point. We used the logistic equation as a model for nestling growth in body mass because it adequately describes the growth of most alcid species for which information is available, and because estimates for the logistic growth rate constant (K) are available for most alcids, allowing for interspecific comparison (Starck & Ricklefs 1998). We used the slope of the tangent at the inflection point as a measure of the maximum instantaneous growth rate. Each nest was considered a grouping unit for

random effects in models, but year was not included as a random effect because the sample size of nests per study year was prohibitively low (Crawley 2002). To account for potential autocorrelation associated with repeated measures of the same chick, we incorporated the autoregressive continuous correlation structure corCAR1 (Pinheiro & Bates 2000). We chose the model that best fit the data using Akaike's Information Criterion corrected for small sample size (AICc) and validated our final model using methods outlined in Pinheiro & Bates (2000).

We analyzed chick meal delivery rates across three years for 16 chicks that survived to at least seven days post-hatch using generalized additive models (GAMs) from the "mgcv" package in R.

We estimated daily survival rates of nests using program MARK (Rotella et al. 2004). We evaluated candidate models in MARK using AICc, and created a confidence set of models by including all models with AICc weights that were greater than 10% of the top model (Burnham & Anderson 2002). We used a model averaging function in MARK to estimate daily survival rates for our confidence set, and methods outlined in Burnham and Anderson (2002) to average coefficient estimates for models in our confidence set.

RESULTS

Nest sites and nest initiation

We discovered 53 active Kittlitz's murrelet nests during 2008-2011, and placed motion-activated cameras near 33 of those nests. All nests were located on the surface of the ground on scree and talus slopes with minimal vegetative cover. Hatch dates were determined either by photography (nests where cameras were deployed) or estimated based on floating eggs at the time of discovery. To account for possible error in estimation of hatch date based on egg-floating, we performed a Student's one-sample *t*-test on the difference between the estimated hatch date and the actual hatch date for 18 nests where cameras were deployed ("camera nests"). The error in estimation of hatch date from egg-floating was between -0.04 and -3.51 days (95% CI). We therefore adjusted our estimates of initiation date by adding 2 d for nests where hatch was not observed by camera to account for this bias. The median estimated nest initiation (egg-laying) date across all years was 3 June, and the range of nest initiation dates was 18 May to 17 July. The distribution of nest initiation dates was skewed toward later dates, with 11% of nests initiated 30 days or more after the median initiation date (Figure 2.1).

Egg size and appearance

Average mass of fresh eggs (within 3 days of laying) measured across all years was 43.2 g (SD = 3.16, n = 8), approximately 18.5% of the average late-breeding/post-breeding adult mass for Kittlitz's murrelets sampled in Kachemak Bay, Alaska in 1990 and 1996 (mean = 233.7 g, SD = 26.9, n = 27; J. F. Piatt, unpublished data). Mean egg

length was 57.7 mm (SD = 2.1, n = 42, range = 53.8–62.7 mm) and mean egg width was 38.2 mm (SD = 1.1, n = 42, range = 36.3–40.8 mm). Egg background color was pale olive-green, mottled with dark brown splotches, as previously described (Day et al. 1999); however, we discovered several eggs that exhibited almost no brown splotching, and one egg that had a tan background, instead of pale olive-green, mottled with dark brown splotching.

Attendance and incubation shifts

We reviewed images from 17 of the 33 camera nests where we detected incubation shift exchanges between the two members of the breeding pair. During incubation, adults visited the nest to exchange incubation duties in relative darkness, an average of 41.0 minutes (SD = 36.1, n = 111 observations) before sunrise (n = 108) or after sunset (n = 3; Figure 2.2). Because we could not rely on the three-minute camera interval to capture all incubation shift exchanges during incubation, we determined the length of adult incubation shifts for only five camera nests where we were able to distinguish between the two breeding adults based on differences in plumage or head morphology. For these nests, 69 of 84 incubation shifts lasted 24 h ± 2 h, two incubation shifts lasted between 30 to 42 h, and 13 incubation shifts lasted between 42.8 and 48.6 h. Mean length of time per incubation shift for all observations was 28.8 h (range = 21.3–48.6 h, n = 84 shifts). We detected at least one incubation shift greater than 42 hours at three of the five nests where the duration of incubation shifts was measured.

Egg neglect was observed on several occasions at two camera nests. One egg was left unattended for unknown reasons on five occasions during its last eight days of development, for a total of approximately 61 h of egg neglect before the egg successfully hatched. At another nest, the incubating parent was flushed twice from the nest by an approaching Sitka black-tailed deer (*Odocoileus hemionus sitkensis,* an introduced species), leading to two periods of egg neglect that each lasted 15–16 h. In addition, at the 28 nests where we deployed cameras immediately after discovering the nest, 11 nests (39%) were unattended for more than six hours following the flush that occurred when the nest was first discovered. In all cases of egg neglect that exceeded six hours, adults returned to their nests during the interval between sunset and sunrise.

Hatching and chick brooding

We estimated hatch date from nest camera images that showed eggshell fragments, frequent movements of the attending adult, or the chick itself. Because of the uncertainty in our estimates of nest initiation date, we were unable to precisely measure the length of the incubation period, although age estimates based on a 30-day incubation period were within ± one day for 10 of 18 camera nests, and within ± four days for 14 of 18 camera nests. In one case where a camera was placed on a nest containing a hole-pipped egg (1 cm diameter), a freshly-hatched chick was observed 23 hours later.

Continuous brooding of the hatchling (brooding without a break greater than 2 h) lasted a mean of 28.8 hours (SD = 9.8, range 14–44 h) after hatching, although this average should be interpreted with caution because the potential error in estimated time

of hatching may have been as great as ± 12 h. Nevertheless, it is clear that at least some chicks were left unattended in an open nest environment after as little as one day of continuous brooding by the parents. At four of 15 camera nests, adults brooded the chick at least once following the cessation of continuous chick brooding. The total length of time that these four adults brooded their chicks following the cessation of continuous brooding was relatively brief (range = 4.5–6.8 h), and brooding bouts always coincided with chick meal (fish) deliveries by a parent.

Chick growth

To describe patterns of nestling growth we plotted chick body mass as a function of age (days post-hatch) for 15 chicks monitored during 2009-2011 (2009, n = 1; 2010, n = 3; 2011, n = 11; Figure 2.3). We included 12 known-age chicks and 3 chicks whose hatch date was estimated by comparing the length of chick primaries with a fitted line of chick primary length as a function of age for chicks whose hatch date was known. Data on age-specific body mass of chicks were fitted to logistic models using methods described by Ricklefs (1983). Briefly, because there was no evidence of a pre-fledging recession in nestling body mass, and because fledging mass was much less that average adult body mass, the logistic model was fitted to all the available data on body mass as a function of age, and the asymptote was not forced through adult body mass.

To test for an effect of nesting year on chick growth rate, we constructed a global model containing a binary year term that compared chicks pooled from 2009 and 2010 vs. chicks from 2011. We pooled nests from 2009 and 2010 to achieve a sample size

large enough for comparison because of small sample sizes in both years; although data were limited, pooling the two years was acceptable because of the similarities in growth rates and nestling periods between 2009 and 2010, compared to 2011. The model containing "year" as a covariate was approximately 10 ΔAICc points greater than the model that was most supported by the data; hence, we rejected our global model in favor of the reduced model that did not include year as a covariate.

For the reduced model, the estimate for the logistic growth rate constant (K) was 0.291 day^{-1} (95% CI = 0.232–0.387); the inflection point (I) of the fitted curve was 6.07 days (95% CI = 5.34–6.79); and the asymptote (A) was 135.5 g (95% CI = 125.7–145.3). Point estimates for parameters in the logistic growth model that contained all growth data were similar to those that included only data from chicks whose hatch date was known (95% CIs: K = 0.222–0.384; I = 5.51–7.19; A = 127.1–148.2). The maximum instantaneous rate of growth, based on point estimates from the model that best fit the data was 9.82 g/d at the inflection point of the fitted curve. The time required for a nestling to grow from 10% to 90% of asymptotic body mass ($t_{10\text{-}90}$; Ricklefs 1967) was 15.1 days, based on point estimates from the best-fit model.

To determine the influence of outliers on the parameter estimates of our logistic growth model, we ran the model after removing the two outliers with the largest residuals individually. Parameter estimates and their standard errors remained similar after removal of each outlier point (Point parameter estimates after removing each outlier: K = 0.288,

0.291; I = 5.83, 6.07; A = 132.0, 135.5). Two chicks that were each weighed about 48 h prior to fledging were 132.5 g and 137.5 g.

Chick feeding

We captured images of a total of 1,232 chick meal (fish) deliveries at 20 nests during 2009-2011. All deliveries consisted of a single fish. For three nests where cameras were deployed with a 1-min photo interval during 2011, only one meal delivery out of a total of 199 detected deliveries involved an adult visiting the nest for less than 3 min. Therefore, we did not use a correction factor in estimating chick meal delivery rates for the remainder of the nests where cameras were programmed to take photos at 3-min intervals.

In contrast to the incubation period, when nearly all adult visits to the nest occurred prior to sunrise, only 24.2% of chick provisioning visits occurred between sunset and sunrise (Figure 2.4). The distribution of provisioning visits with respect to time of day was bimodal, with peaks occurring 42 min after sunrise and 19 min after sunset (Figure 2.4). Chick meal deliveries occurred most frequently during the morning, with 41.8% of all recorded deliveries occurring within the 4-h period centered on 42 min after sunrise. Chick meal deliveries were less frequent in the evening, with 27.4% of all deliveries occurring during the 4-h period centered on 19 min after sunset. Chick meal deliveries during the daylight hours between the morning 4-h peak period and the evening 4-h peak period accounted for 30.2% of all recorded deliveries. For cases where cameras were motion-activated during both the arrival and the departure of an adult, and,

hence, exact times of arrival and departure were known, adults stood at the rim of the nest for an average of 12.6 min before transferring a fish meal to the chick (n = 97 motion detected deliveries, SD = 6.9, range = 3.6–48.2 min).

For analysis of chick meal delivery rates we pooled nests from 2009 and 2010 (n = 2 for each year) to achieve a sufficient sample size for comparison with 2011. We considered this merging of samples as acceptable because chick meal delivery rates were nearly identical between these two years (Table 2.1), and because the nestling period (time from hatching to fledging) was similar between one nest that was monitored in 2009 and three nests that were monitored in 2010 (two camera nests and one non-camera nest; range = 22–24 days). Chicks in 2011 received significantly more fish throughout the nestling period ($P < 0.001$) than pooled chicks from 2009 and 2010 (Figure 2.5). The estimated peak in chick meal delivery rates was on day 16 post-hatch for all three years (Figure 2.5). Chicks were fed an average of 4.2 fish/d (95% CI: 3.71–4.70) during the peak of chick provisioning in 2009 and 2010, and an average of 5.1 fish/d (95% CI: 4.68–5.43) during peak chick provisioning in 2011. Averaged over the entire nestling period, chicks were fed 3.9 fish/d (95% CI: 3.38–4.42) during 2009 and 2010, and 4.8 fish/d (95% CI: 4.34–5.21) in 2011.

Diet composition

We identified 998 (81.0%) of all the meals delivered to chicks at camera nests (n = 1,232 forage fish) either to species (i.e., Pacific sand lance, capelin [*Mallotus villosus*], Pacific herring [*Clupea pallasi*]) or to family (i.e., Salmonidae). We were not able to

identify the remaining 234 (19.0%) of chick meals because of poor image quality. We did not include "unknown" fish in a subsequent analysis of the proportion of fish species delivered to chicks. There was no significant among-year difference in the proportion of different fish species delivered to chicks ($P = 0.47$, Fisher's exact test). During 2009-2011, the percentage of forage fish types in identifiable chick meals was: 91.7% Pacific sand lance, 7.6% capelin, 0.4% Pacific herring, and 0.2% salmonids.

We estimated the size class of 1,183 fish that were delivered as chick meals during 2009-2011 (Table 2.2). There was no significant difference in the proportions of different size classes of fish delivered to chicks across years ($P = 0.1018$, Fisher's exact test). During 2009-2011, 70.8% of fish delivered to chicks were in the 12–16 cm total length size class, and 27.4% of fish were in the 8–12 cm total length size class. The range in size of fish was large; the smallest fish was approximately 6 cm in length and the largest was ca. 17 cm in length. Results of a generalized additive model (GAM) indicated that the average size of fish provisioned to nestlings increased significantly during the first 5 days of chick development for pooled nests ($P < 0.0001$, n = 16 chicks), but remained relatively constant thereafter (Figure 2.6).

Fledging

We summarized data on chick fledging for all nests where information was available (n = 9 nests; Table 2.3). Mean chick age at fledging was 24.8 days across all years (SD = 2.31, n = 8 chicks). Exact age at fledging was known for 5 of the 8 chicks because cameras were deployed at their nests before hatching; the age of the other 3

chicks was not known precisely because their hatch date was estimated based on the chick's wing chord length at the time the nest was discovered (Table 2.3). There was a significant difference in the length of the nestling period between 2009/2010 and 2011 (P = 0.001, 95% CI = 2.34–5.65 d; t-test). Mean age at fledging was 22.8 d in 2009 and 2010 (SD = 0.96, n = 4), and 26.6 d in 2011 (SD = 0.95, n = 4; Table 2.3). Chicks that fledged in 2009 and 2010 were fed an average total of 84.8 fish during the nestling period (SD = 3.69, n = 3), whereas chicks that fledged in 2011 were fed an average total of 141.1 fish during the nestling period (SD = 30.7, n = 4, Table 2.3).

Nest fate and nesting success

Nine chicks fledged from the total of 53 monitored active nests (17% fledging success). To determine daily survival rates of murrelet nests, we incorporated overall nest age (days post-laying), nest stage (incubation vs. chick-rearing), nestling age (days post-hatching), calendar date, year, nest search area (n = 4), camera treatment (nest camera present or absent), and quadratic terms for nest age and calendar date into 20 different nest survival models in program MARK. Our confidence set of models was comprised of four models within ca. 4 ΔAICc units of the model best supported by the data (Table 2.4). The odds of nest survival were significantly negatively associated with the year 2008 and with the chick-rearing period (conditional odds ratios < 1.0; Table 2.4).

Estimates of average daily nest survival from our confidence set of models indicated an abrupt decline in daily survival rate at hatching, with no significant trend prior to or following hatching (Figure 2.7). Assuming an average 55-d nesting period

(incubation and chick-rearing combined), the average overall survival rate for nests as derived from the confidence set of models was 0.0760 (95% CI = 0.0044–0.2750) during 2008-2011. Camera deployment at a nest had no detectible effect on daily nest survival rate, based on the original confidence set of models (Table 2.5). Moreover, the proportion of camera nests where a chick was fledged (0.21) was higher than the proportion of non-camera nests where a chick was fledged (0.10). Consequently, we created a second confidence set of models that did not include a camera term in order to derive a final estimate of nest survival rate. Based on this confidence set, the average overall annual nest survival rate, or number of chicks fledged per pair (assuming no successful renest attempts), was 0.0933 (95% CI = 0.0067–0.2991). Although a model that assumed constant daily survival rates (maximum likelihood Mayfield estimate) was not supported by our model selection procedure, for purposes of comparison the estimate of average overall nest survival rate, based on a model of constant daily nest survival, was 0.0944 (95% CI = 0.0435-0.1777). Based on these analyses, the chances that a nesting attempt by Kittlitz's murrelets in our study area would produce a fledgling were almost certainly less than 30%.

Depredation of nest contents was the most frequent cause of nest failure in all four years of the study (Table 2.6). Depredation events detected on-camera or by revisiting an active nest and finding it empty accounted for 47% of all nest fates. Depredation of a nest during the incubation stage accounted for 34% of all nest fates and depredation during the chick-rearing stage accounted for 13% of all nest fates. Of the 12 nests where depredation

of the nest contents was documented on-camera, 10 were depredated by red foxes (*Vulpes vulpes*); we were unable to identify the nest predator for the other two depredated nests because the predator failed to trigger the camera while within the camera's field-of-view.

Eleven chicks were found dead on monitored nests during 2009-2011 (Table 2.6), and one inactive nest was discovered containing a recently deceased chick in 2010. Six chicks found dead on the nest in 2011 were preserved in 70% ethanol and subsequently necropsied at the USGS National Wildlife Health Center (Madison, WI, USA). The necropsy report indicated that the general body condition of all six chicks was fair to good, suggesting adequate nutrition. Five of the six necropsied chicks had significant lesions in the gut and other internal organs associated with infection by nematode-like endoparasites that were unidentifiable because of the generally decomposed condition of the chick specimens. The lesions from endoparasites were significant and, for at least one of the six dead chicks, was evidently the cause of death (USGS National Wildlife Health Center 2012). Further analysis indicated that saxitoxin, a potent neurotoxin produced by certain species of dinoflagellates, was present in the gut contents of four of five necropsied chicks collected in 2011 (the sixth chick did not include a sufficient sample of gut contents for analysis). As part of an ongoing study, the gut contents and livers of three Kittlitz's murrelet chicks found dead in the nest were collected in the study area during 2012; all three chicks had high levels of saxitoxin. These findings suggest that saxitoxin may also have been a significant contributing factor to chick mortality during 2011 (V. I. Shearn-Bochsler, pers. comm.).

Seven eggs were abandoned during 2008-2011. Five of these eggs were determined to be addled upon our final nest visit, did not appear to contain a developing embryo, and may have been infertile. The remaining two eggs contained embryos that were approximately 5 days and 25 days into embryonic development. The first of these two eggs was abandoned on 10 July 2008, and when checked 5 days later the egg had a 1 cm wide hole in the shell. The second was abandoned on 11 August 2011, and represented the latest incubation activity observed during the four-year study.

DISCUSSION

Egg mass and chick growth and development

Characteristics of Kittlitz's murrelet eggs and the rate of chick growth and development are outliers compared to the other 15 species of semi-precocial alcids. Mean egg mass from our study was 18.5% of average post-breeding adult body mass, among the highest of the semi-precocial alcids (Table 2.7).

The growth rate constant (K) of Kittlitz's murrelet chicks on Kodiak Island, (0.291) was much greater than that of Kittlitz's murrelet chicks on Agattu Island in the western Aleutians (K = 0.096, n = 4; Kaler et al. 2009); the growth rate data from Agattu Island are the only other data available for intraspecific comparisons of chick growth rates. Associated with the relatively high chick growth rate on Kodiak Island, the length of the nestling period (hatching to fledging) was less on Kodiak Island compared with Agattu Island (22–28 d vs. 30 d; Kaler et al. 2009, n = 2 chicks), although the average

nestling period on Kodiak Island (24.8 d) is consistent with two nestling periods reported by Day et al. (1999).

Body mass of Kittlitz's murrelet chicks at fledging was 135.5 g in our study (based on the asymptote of the fitted logistic equation), 58% of average adult body mass. This is considerably more than the 40% of adult body mass at fledging reported by Day et al. (1983) for a fledgling discovered on the Kenai Peninsula, Alaska, or the average of 47% of adult body mass at fledging reported by Kaler et al. (2009) for chicks on Agattu Island.

Compared to chicks of other semi-precocial alcids, Kittlitz's murrelet chicks in this study displayed the highest logistic growth rate of any species, both on an absolute scale (Table 2.7) and when scaled to asymptotic nestling mass (Figure 2.8), Kittlitz's murrelet chicks also displayed the shortest average nestling period and among the lowest fledging mass (% adult body mass) compared to other semi-precocial alcids (Figure 2.9).

While the scope of inference for this study was limited by small sample sizes and restricted geographic and temporal scales, our data indicate that comparatively high growth and development rates are possible for Kittlitz's murrelet nestlings, but it is unclear whether such rapid growth is the norm for the species given the slow growth observed for chicks at Agattu Island (Kaler et al. 2009). Comparisons with the *Cepphus* guillemots, which comprise the inshore-foraging semi-precocial alcids, along with the *Brachyramphus* murrelets (Lack 1968), suggest that high growth and development rates

for Kittlitz's murrelet on Kodiak Island are most similar to growth rates for other inshore-foraging alcids (Figure 2.8).

The generally higher growth rates observed among inshore-foraging seabirds, as compared with offshore-foraging seabirds, is hypothesized to be a consequence of higher provisioning rates enabled by relatively short foraging trips (Lack 1968; Cody 1973); this is illustrated by the large number of deliveries made by *Cepphus* guillemots compared to other semi-precocial alcids (Table 2.7). Additionally, there is speculation that limitations in the availability of secure nest sites near inshore foraging areas may result in higher numbers of available forage fish in such areas owing to reduced competition (Cody 1973; Ricklefs 1990). Unlike *Cepphus* guillemots, which have relatively large body sizes and are the only semi-precocial alcids that lay two-egg clutches, *Brachyramphus* murrelets are small in body size and lay a single, relatively large egg. Such traits would be expected to reflect lower parental costs related to chick-rearing because smaller chicks require less total energy for maintenance and tissue growth, although these savings may be offset to some degree by increased thermoregulatory costs. While the abbreviated brooding period for Kittlitz's murrelet nestlings would likely increase thermoregulatory costs for nestlings, it may provide a net energetic benefit to the parent-offspring unit because it allows both parents to simultaneously provision the nestling soon after it hatches. As a likely result of restricting energy demand at the nest (i.e., one small, thermally independent chick that fledges at low asymptotic mass), Kittlitz's murrelets on Kodiak

Island were able to raise rapidly-growing offspring without making large numbers of deliveries, as do *Cepphus* guillemots.

Moreover, evidence from a wide variety of avian species suggests that high growth rates significantly reduce cumulative nestling energy requirements (Weathers 1992). Thus, a rapid growth rate itself would also tend to reduce overall parental investment by reducing the total amount of food delivered to the nest in order to fledge a chick. With the apparent high risk of nest predation experienced by Kittlitz's murrelet nests on Kodiak Island, as well as potential parental energy constraints related to inland nesting (Hatch 2011), such a coupling of relatively low nest provisioning rates with rapid chick growth and development would clearly be adaptive.

Diet composition and rate and timing of provisioning

Sand lance and capelin accounted for nearly all fish delivered to Kittlitz's murrelet chicks. Both of these forage fish species are among the most lipid-rich species in the northern Gulf of Alaska (Anthony et al. 2000). The high degree of specialization in the diet for Kittlitz's murrelet chicks on Kodiak Island suggests that this strategy plays an important role in nesting success. Kittlitz's murrelets on Kodiak Island, along with its congener the marbled murrelet, make far fewer provisioning flights to their nests than do other fish-provisioning semi-precocial alcids (Figure 2.10). Such a low number of deliveries would be adaptive given the apparent high risk of nest predation for *Brachyramphus* nests and the elevated predation risk to adults that is likely associated with commuting to inland nest sites. The availability of high quality forage may be a

crucial factor that allows adults to successfully provision offspring with a minimum number of nest visits, thus minimizing risk at the nest site as well as reducing parental investment.

While there was no detectible inter-annual difference in the size or species composition of fish delivered to chicks, inter-annual differences in chick provisioning rates and fledging age suggest a difference in the quality of fish delivered to chicks in 2011 compared to 2009-10. Chicks in 2011 were provisioned an average of 20.2% more fish per day during peak provisioning than chicks in 2009 and 2010; however, chicks took an average of 4 days longer to fledge in 2011. Although our best-fit growth model did not contain year as a covariate, small sample sizes, especially in 2009 and 2010, may have precluded detection of differences in chick growth rates among years. The pattern of residuals for chick body mass relative to the fitted curve from our best-fit model, however, suggests that chick growth rates were lower in 2011 relative to 2009 and 2010 (Figure 2.3). For chicks in 2009 and 2010, only 20% of mass measurements were below the fitted curve, while in 2011 57% of mass measurements were below the fitted curve. Weather data across all four study years were similar, suggesting that increased thermoregulatory costs were not responsible for higher energy requirements and potentially slower growth for chicks in 2011. Although chicks did show evidence of pathogenic endoparasite and saxitoxin burdens in 2011, and thus might be expected to have displayed slower growth, we cannot be certain that some chicks in previous years of the study did not experience the same disease factors.

Forage fish quality can vary on an annual basis (Anthony et al. 2000; Williams & Buck 2010), and such variation can have major effects on seabird productivity (Wanless et al. 2005; Williams & Buck 2010). Pacific sand lance, the major food source for Kittlitz's murrelet chicks in all study years, display considerable inter-annual variation in lipid content (Williams & Buck 2010). Thus, it is possible that inter-annual variation in the nutritional quality (lipid content) of sand lance was responsible for the inter-annual difference in chick growth and development rates, despite the compensatory increase in chick meal delivery rates. Whatever the cause of higher chick meal delivery rates in 2011, adults that successfully fledged chicks made an average of 66% more deliveries to chicks before fledging in 2011 compared with 2009-10 (Table 2.3). Such an increase in nest visits presumably comes at the risk of nest predation, and likely increases the risk of parental mortality (Ydenberg 1989; Clark & Ydenberg 1990; Ghalambor & Martin 2001), and certainly increases the energetic burden on adults.

A large percentage (ca. 30%) of chick meal deliveries occurred between the peak morning and the peak evening delivery periods. However, nest visits during incubation and chick fledging occurred almost exclusively before sunrise or after sunset, which is more consistent with a strategy of predator avoidance (Gaston & Jones 1998; Cody 1973). It is unclear why so many chick meal deliveries were made during daylight hours, especially when considering that the marbled murrelet–the best-known *Brachyramphus* species–appears to provision infrequently during diurnal periods (Nelson & Hamer 1995a). It is possible that the temporal pattern of provisioning visits on Kodiak Island

reflected forage fish accessibility. Alternatively, diurnal meal deliveries could represent a trade-off between predation risk and high chick energy demands that are necessary for rapid growth and development.

Nest survival

Our estimate of nest success for Kittlitz's murrelets was 0.093, a nest survival rate lower than that of 18 other alcid species, whose nest success rates range between 0.33 and 0.86 (reviewed in De Santo & Nelson 1995). The 95% confidence interval for Kittlitz's murrelet nest success (0.007 - 0.299) appears similar to the average nest success in several studies of marbled murrelets (0.07 - 0.28; reviewed in Nelson & Hamer 1995b; Peery et al. 2004; Hébert et al. 2006; Barbaree 2011), although one marbled murrelet study reported probable annual nest success of at least 50% (Zharikov et al. 2006). The possibility that the discovery and monitoring of active alcid nests may result in lower nest success has been noted in other studies (Major 1990; Piatt et al. 1990). However, we concluded that our monitoring had a negligible effect due to limited number of visits and apparent absence of a temporal relationship between visits and depredation events.

There is some evidence that nests of black guillemots (*Cepphus grylle*), least auklets (*Aethia pusilla*), and Atlantic puffins (*Fratercula arctica*) are more likely to be abandoned or experience hatching failure as a result of the activities of researchers near the nest (Cairns 1980; Piatt et al. 1990; Rodway et al. 1996). The relatively high rate of egg abandonment during our study may have been a consequence of our activities. In contrast to the above studies, however, we did not visit nests during the incubation stage

following nest discovery in order to avoid disturbance to incubating adults. In addition, the high rates of egg abandonment observed for marbled murrelets and Xantus's murrelets (*Synthliboramphus hypoleucus*) have been attributed to other causes (Nelson & Hamer 1995b; Wolf et al. 2005).

The high rate of chick death encountered during our study is difficult to explain without considering disease as a possible cause. Kaler et al. (2009) reported that 3 out of 11 chicks monitored on Agattu Island apparently died of exposure during their study, but exposure does not seem to explain most chick deaths on Kodiak Island. Chicks on Kodiak Island died at all stages of development and during a variety of weather conditions. Most dead chicks discovered on Kodiak Island were in apparently good body condition at the time of death. The effect of parasitic disease and saxitoxin toxicity on chick survival should be investigated further, given the unexpected conclusions of the pathology report from the USGS National Wildlife Health Center (2012), and preliminary conclusions regarding the discovery of saxitoxin in chicks (V. I. Shearn-Bochsler, pers. comm.).

Red foxes appeared to be important predators of Kittlitz's murrelet nests within our study area. Although red foxes are present in inland habitats across most of the presumed nesting range of Kittlitz's murrelets in Alaska, it is unclear whether they pose a significant threat to nests in other areas, especially in extremely rugged, glaciated terrain. The same characteristics that made nest sites on Kodiak Island relatively easy for nest searchers to access may also mean that predators are present at levels much higher than

might be expected in other potential nesting habitats, especially because areas of nesting habitat within the study area were relatively small and were situated in close proximity to vegetated lowlands, where mammalian predators were commonly observed (see Chapter 3). While it is possible that camera placement may have increased the risk of nest predation, our models suggest that this was not the case. The two most competitive models in our confidence set included the presence of a nest camera as a covariate, but the parameter estimate was positive, not negative, and the confidence limits widely overlapped zero. Predictions for nest survival in program MARK, therefore, were higher across the nesting season for camera nests than for non-camera nests, but not significantly so.

Conclusions

The low nest survival rate measured for Kittlitz's murrelets nesting on Kodiak Island and the variety of reproductive traits that seem consistent with minimizing nest predation rates suggest that the nests of Kittlitz's murrelets are high-risk environments for nestlings compared to non-*Brachyramphus* alcids. Consistent with this prediction that Kittlitz's murrelet nestlings are exposed to a high-risk environment, adults provisioned their chicks with low numbers of high-quality forage fish, and chicks grew at very high rates and had very short nestling periods. Assuming that this rapid growth and development is adaptive by minimizing exposure to a high-risk nesting environment, the availability and reliability of high-lipid, energy-dense prey may be crucial for minimizing

the risks incurred by nestlings and parents alike, and critical for overall reproductive success and population productivity.

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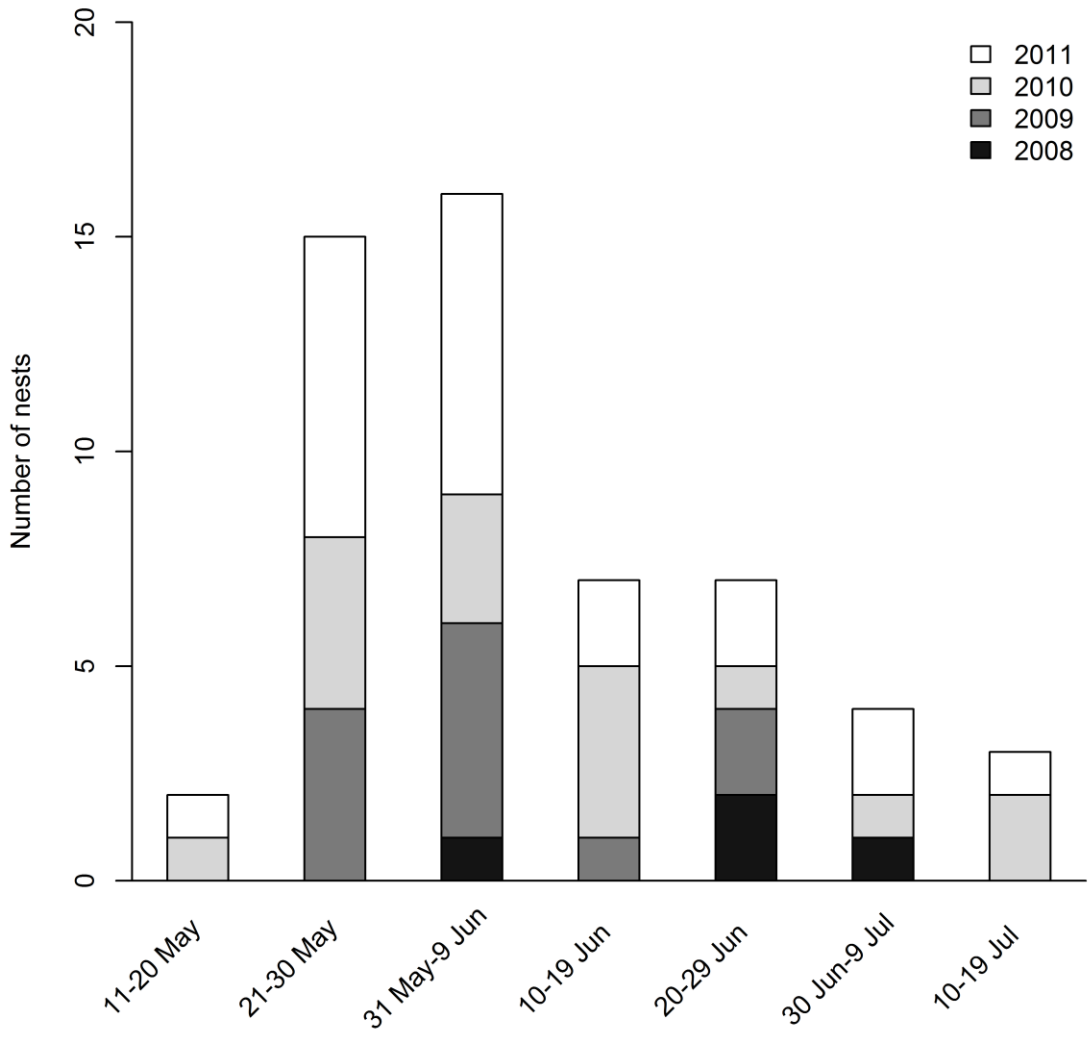

Figure 2.1. Estimated egg-laying dates for Kittlitz's murrelets nesting on Kodiak Island, Alaska during 2008-2011.

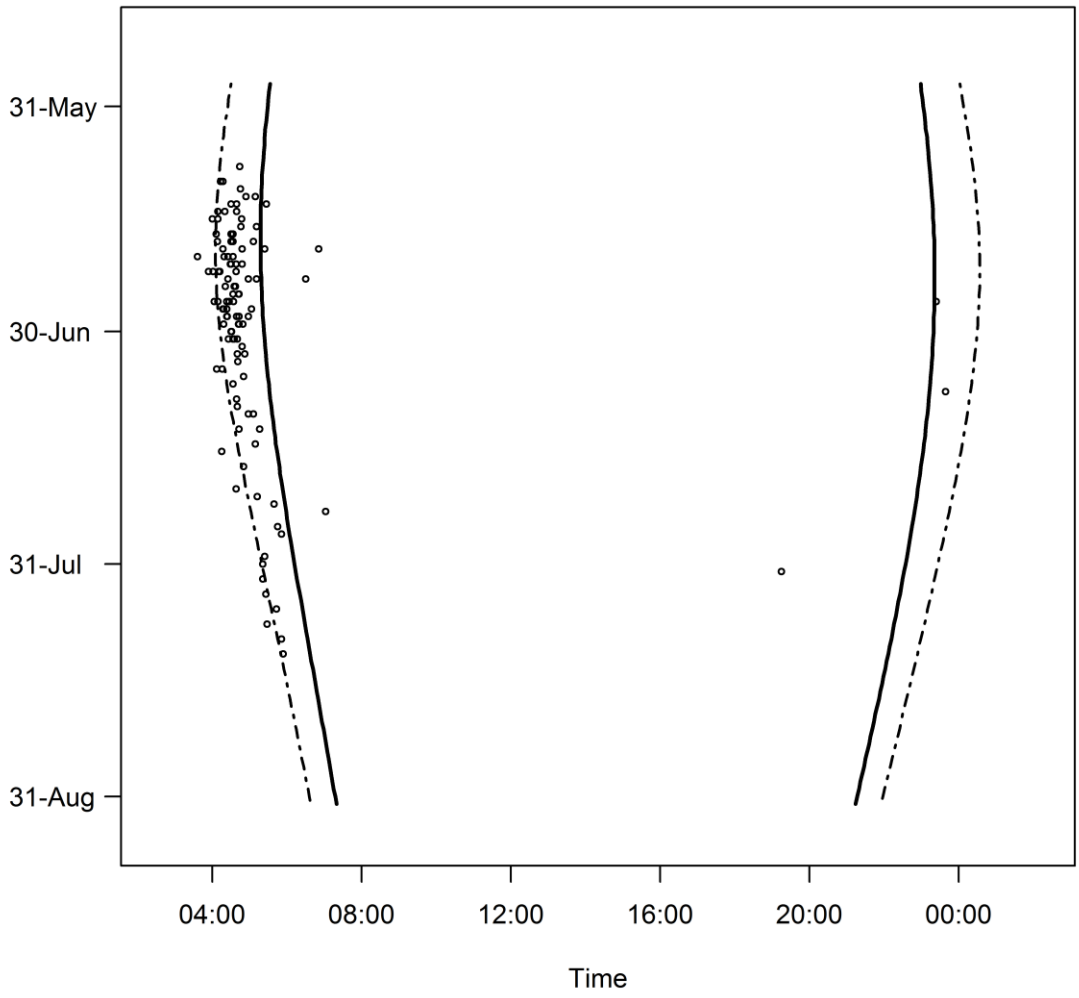

Figure 2.2. Timing of incubation shift exchanges by breeding pairs of Kittlitz's murrelets at 17 nests on Kodiak Island, Alaska during 2009-2011. Solid lines represent sunrise and sunset; dashed lines represent civil twilight.

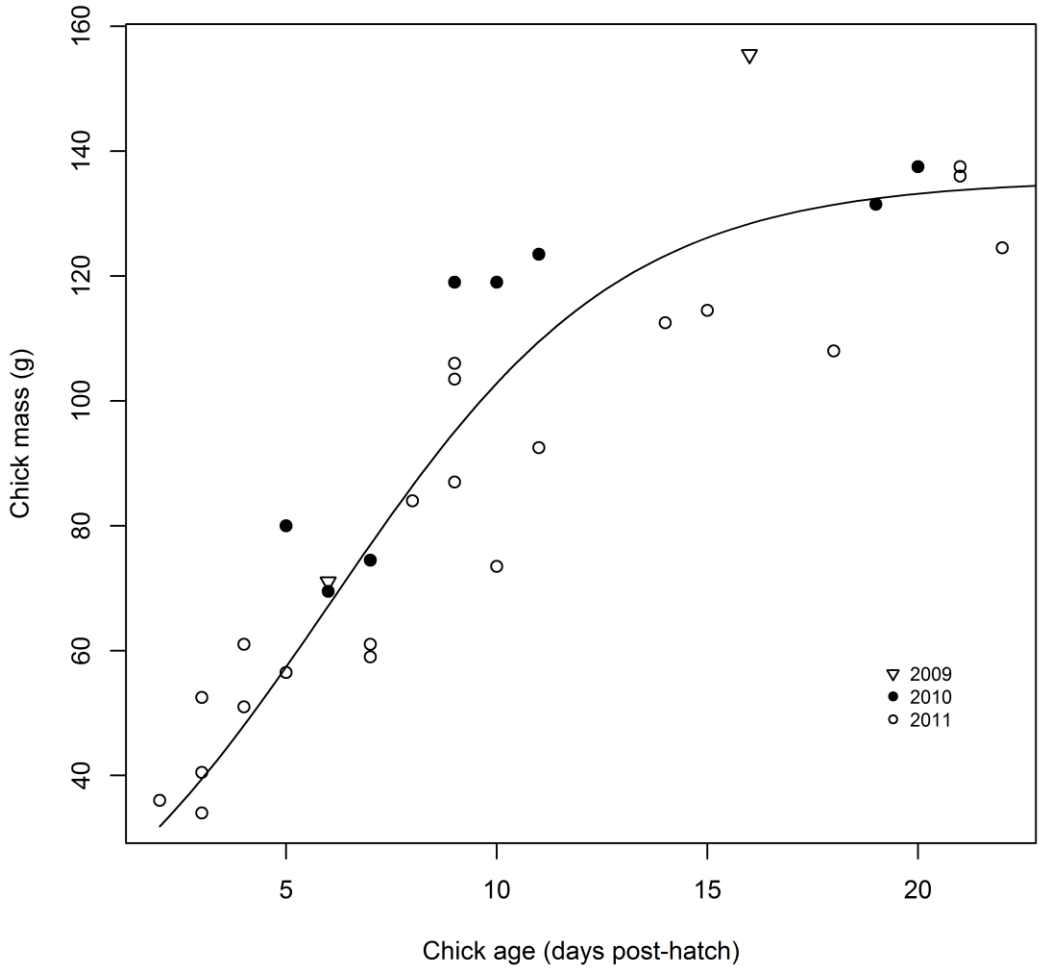

Figure 2.3. Body mass of Kittlitz's murrelet chicks as a function of age on Kodiak Island, Alaska during 2009-2011. The curve represents a logistic model fitted to the data points.

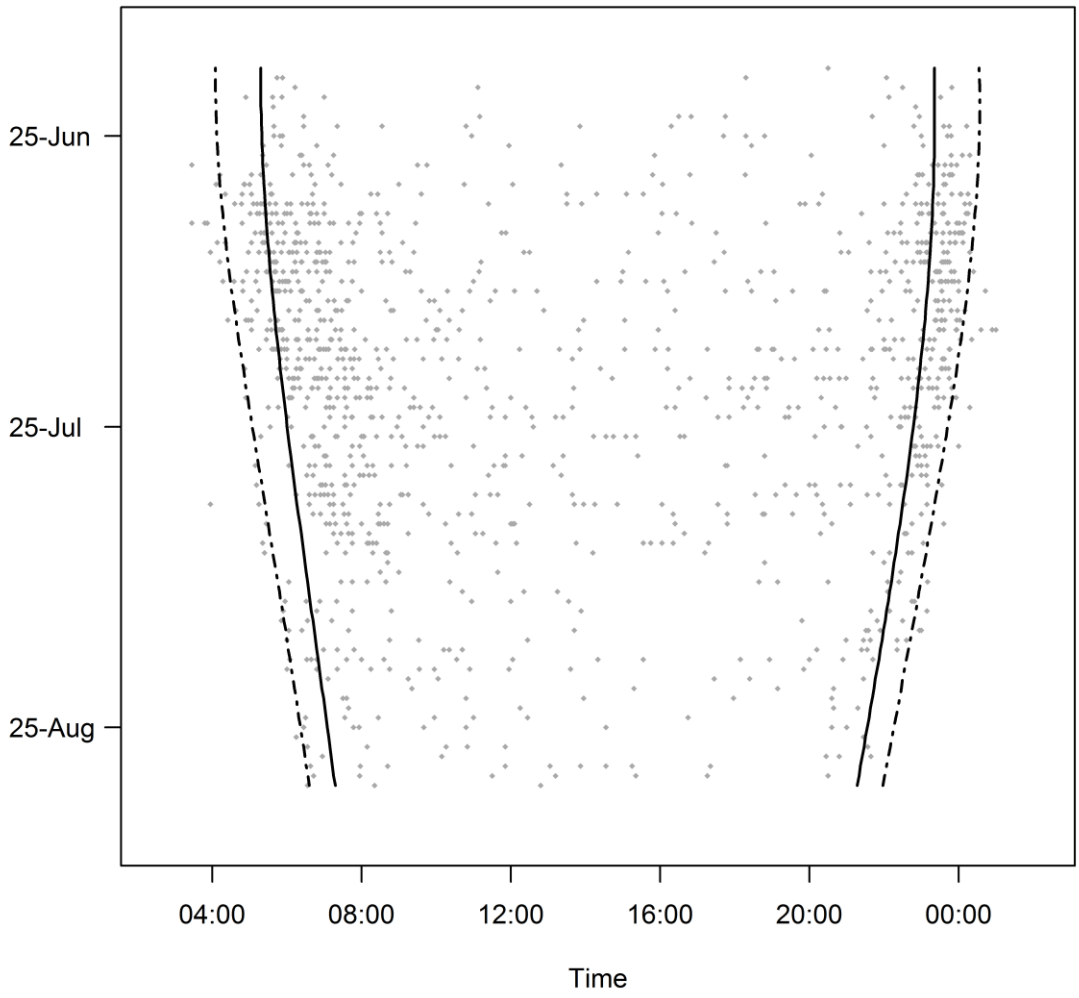

Figure 2.4. Timing of visits to the nest by adult Kittlitz's murrelets provisioning young on Kodiak Island, Alaska during 2009-2011 (n = 20 nests). Solid lines represent sunrise and sunset; dashed lines represent civil twilight.

Table 2.1. Summary of meal delivery rates to Kittlitz's murrelet chicks on Kodiak Island, Alaska during 2009-2011.

Year	Mean No. of Fish/Day	SD	Range	# Chick Days	# Nests
2009	3.83	1.60	1–7	30	2
2010	3.92	1.53	0–7	39	2
2011	4.71	1.96	1–12	198	12

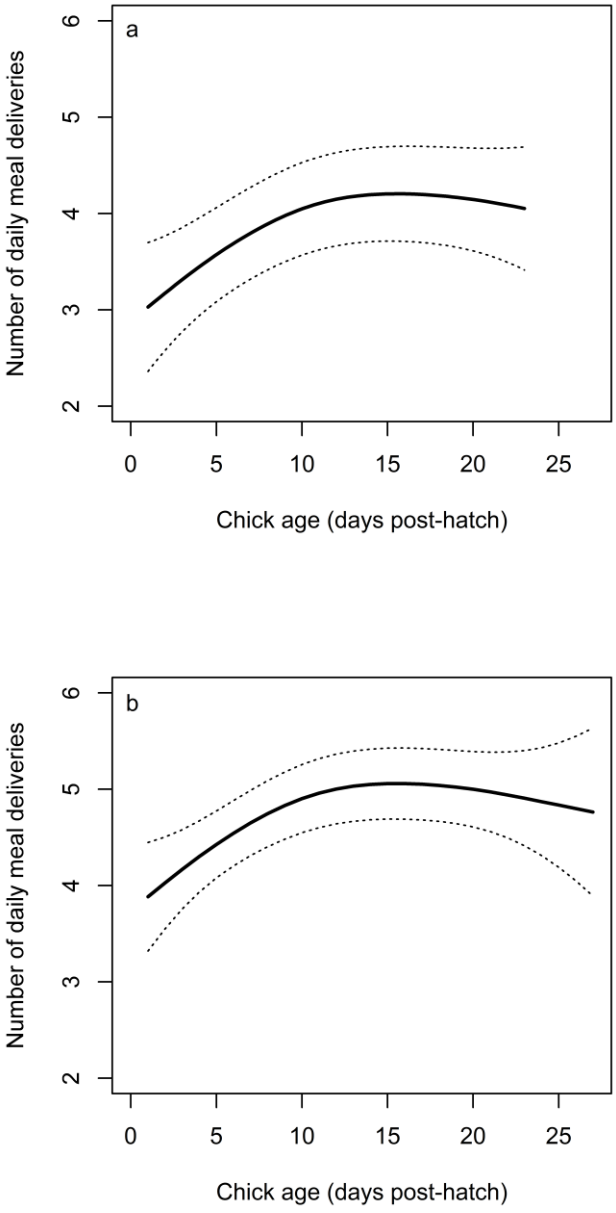

Figure 2.5. Average meal delivery rates to nestling Kittlitz's murrelets by their parents on Kodiak Island, Alaska during 2009 and 2010 (a; n = 4 chicks) and during 2011 (b; n = 12 chicks).

Table 2.2. Number and proportion (in parentheses) of size classes of fish delivered to Kittlitz's murrelet chicks on Kodiak Island, Alaska during 2009-2011. Fish length = total length.

Year	< 8 cm	8–12 cm	12–16 cm	> 16 cm
2009	0 (0)	32 (0.28)	82 (0.72)	0 (0)
2010	5 (0.03)	43 (0.25)	122 (0.71)	2 (0.01)
2011	4 (0.005)	250 (0.28)	633 (0.71)	10 (0.01)
Total	9 (0.008)	325 (0.27)	837 (0.71)	12 (0.01)

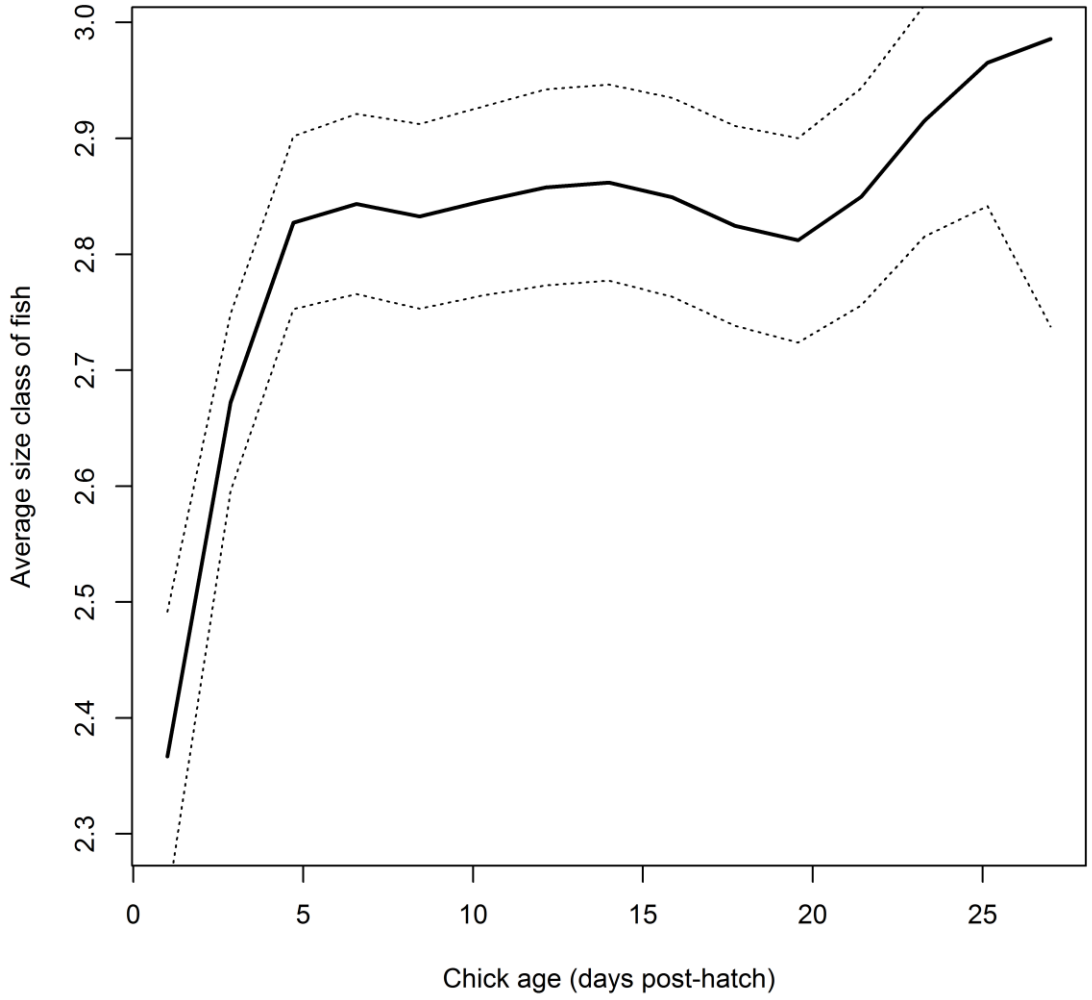

Figure 2.6. Average size class of fish delivered to 16 Kittlitz's murrelet chicks on Kodiak Island, Alaska during 2009-2011. Size class 2 fish are 8–12 cm total length, and size class 3 fish are 12–16 cm total length.

Table 2.3. Summary of chick age at fledging and meals provisioned to chicks pre-fledging at Kittlitz's murrelet nests on Kodiak Island, Alaska during 2009-2011.

Nest ID	Nestling period (d)	Chick meal delivery rate (fish/day)	Total number of fish delivered during the nestling period	Fledging date	Fledging time of day
0906[a]	24	3.7	85	7/23/2009	6 min before sunset
1006[b,c]	23	N/A	N/A	8/5/2010	N/A
1011[a]	22	3.68	81	8/7/2010	42 min before sunrise
1013[a]	22	4.11	88[e]	8/7/2010	31 min after sunset
1014[d]	N/A	N/A	N/A	7/28/2010	N/A
1108[a]	26	4.64	116	8/7/2011	38 min after sunset
1115[a]	28	5.5	154	8/20/2011	33 min before sunrise
1116[b]	26	4.64	116[e]	7/25/2011	1 min after sunset
1122[b]	27	5.82	178[e]	9/1/2011	3 h 43 min. before sunrise
Mean (SD, n nests)	24.75 (2.31, 8)	4.58 (0.83, 7)	116.9 (37.1, 7)	--	--

[a]Nests where date of hatch was confirmed from camera images or nest was discovered during egg pipping stage.
[b]Nests where date of hatch was estimated by comparison of chick wing chord length with that of known-age chicks.
[c]Non-camera nest; fledging date confirmed by two nest checks ~12 h apart, before and after fledging.
[d]Chick fledged when nest discovered.
[e]Numbers of fish delivered prior to camera installation were estimated from nest-specific delivery rates after camera installation.

Table 2.4. Confidence set of nest survival models for Kittlitz's murrelet nests on Kodiak Island, Alaska during 2008-2011.

Model	AICc	ΔAICc	AICc weights	Number of parameters	Confidence set AICc weights
Nest age[a] + nest stage[b] + nestling age[c] + camera[d] + year[e]	268.773	0	0.37948	8	0.44
Nest age + nest stage + nestling age + camera	268.832	0.059	0.36847	5	0.43
Nest age + nest stage + nestling age + year	272.271	3.500	0.06599	7	0.08
Nest age + nest age^2 + camera + year	272.902	4.130	0.04813	7	0.06

[a]Age of nest (days post-laying) .
[b]Indicator variable for incubation (0) or chick-rearing (1).
[c]Age of nestling; coded as an interaction term. Inclusion in models suggests difference in slope for survival of eggs vs. chicks.
[d]Indicator variable for nest without camera (0) or with camera (1).
[e]Factor variable for study year. Reference group is 2011.

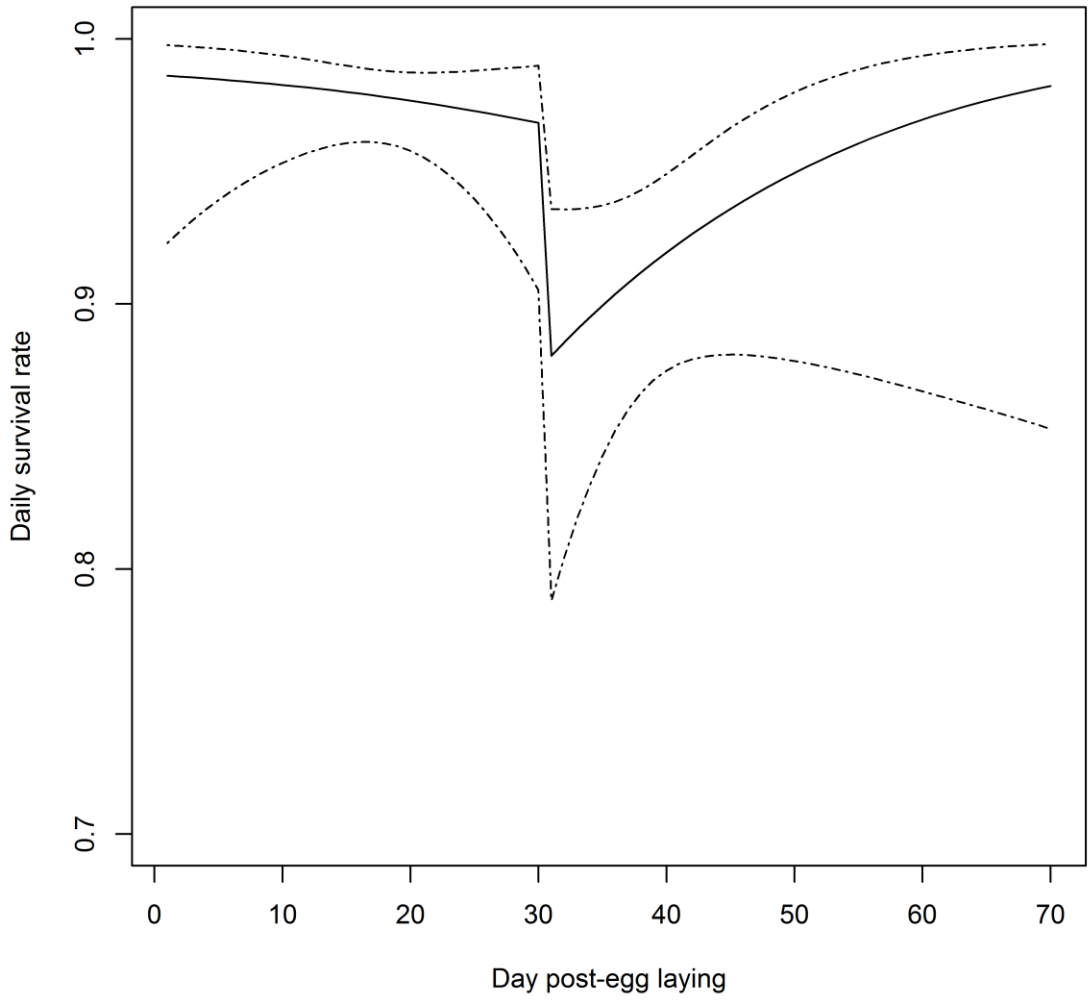

Figure 2.7. Daily survival for nests of Kittlitz's murrelets on Kodiak Island, Alaska during 2008-2011. Day 30 represents the average day of chick-hatching (average incubation period). Solid line represents point estimates of daily nest survival rate; dashed lines represent the upper and lower 95% confidence limits.

Table 2.5. Averaged parameter estimates for the confidence set of four models to explain variation in daily survival rate of Kittlitz's murrelet nests on Kodiak Island, Alaska during 2008-2011. Rows in bold indicate variables with 95% confidence intervals that do not include equal odds (i.e., Conditional odds ratio = 1)

Variable	$\hat{\beta}$	SE	Conditional odds ratio*	Conditional odds ratio 95% lower CL	Conditional odds ratio 95% upper CL
Intercept	**3.920**	**1.055**	**50.39**	**6.369**	**398.6**
Nest age	-0.036	0.053	0.965	0.871	1.070
Nest age^2	0.0001	0.000	1.0001	0.9999	1.0004
Nest stage	**-3.675**	**1.475**	**0.025**	**0.001**	**0.456**
Nestling age	0.075	0.052	1.077	0.974	1.192
Camera	0.887	2.097	2.428	0.040	148.1
2008	**-1.696**	**0.484**	**0.183**	**0.071**	**0.474**
2009	-0.460	0.277	0.631	0.367	1.087
2010	0.151	0.268	1.163	0.688	1.968

*Odds ratio = e^$\hat{\beta}$

Table 2.6. Fates of Kittlitz's murrelet nests on Kodiak Island, Alaska during 2008-2011.

Nest Fate	2008	2009	2010	2011	2008-2011	% 2008-2011
Depredated/nest empty	2	8	6	9	25	47
Chick found dead	0	1	2	8	11	21
Nest abandoned	1	2	3	1	7	13
Unknown	1	0	0	0	1	2
Chick fledged	0	1	4	4	9	17
Total	4	12	15	22	53	100

Table 2.7. Mean estimates of reproductive parameters for 15 species of semi-precocial alcids (Family: Alcidae).

ID	Species	Adult mass (g)	Egg mass (% adult body mass)	Fledging mass (% adult mass)	Period of continuous brooding (d)	K (logistic)	Asymptotic chick mass (g)	Nestling period	Deliveries · day^{-1}	Delivery strategy*	Mean annual nest success (%)
1	Dovekie[1]	164	19	75	2-4	0.239	112	27	6.8	MZ	50
2	Spectacled guillemot[2]	490	11	84	?	?	493	35	13.9	S	?
3	Black guillemot[3]	406	12.5	94	3-5	0.135	430	37	16.4	S	45
4	Pigeon guillemot[4]	490	11	90	3	0.1515	460	38	16.2	S	47
KIMU	Kittlitz's murrelet[5]	234	18.5	58	0.5-2	0.291	135.5	24.8	4.3	S	9
MAMU	Marbled murrelet[6]	221	18	67	0.5-3	0.187[†]	145	29	3.2	S	7-50[††]
7	Crested auklet[7]	272	14	87	1-2	0.197	254	33	3	MZ	42
8	Least auklet[8]	86	22	100	3-6	0.2415	93	29	3.6	MZ	66
9	Whiskered auklet[9]	121	?	92	4-5	?	113	40	3	MZ	86
10	Cassin's auklet[10]	177	16	88	4	0.156	155	43	2	MZ	60
11	Parakeet auklet[11]	297	14	80	7	0.183	239	35	2	MZ	?
12	Rhinoceros auklet[12]	533	15	61	4	0.104	399	52	3	MF	56
13	Tufted puffin[13]	773	12	65	6-7	0.1135	490	49	4	MF	44
14	Horned puffin[14]	612	10	65	1-4	0.1095	400	38	4.5	MF	53
15	Atlantic puffin[15]	460	13	65	?	0.1325	321	46	3.8	MF	53

Table 2.7 (Continued)

Sources: Barbaree 2011; Day et al. 1999; De Santo & Nelson 1995; Gaston & Jones 1998; Harris & Birkhead 1985; Hébert et al. 2006; Hirsch et al. 1981; Kitaysky 1994; Minami et al. 1995; Peery et al. 2004; Piatt et al. 1990; Roby & Brink 1986; Simons 1980; Starck & Ricklefs 1998; Ydenberg 1989; Zharikov et al. 2006; this study.

* MZ = multiple zooplankton; S = single fish; MF = multiple fish.
† n = 2 nests (Simons 1980; Hirsch et al. 1981)
†† Nest survival estimated at 50% for nests described in Zharikov et al. 2006, where nest survival was reported as 63% at day 20 of the nestling period for 139 nests, ca. 9 days prior to fledging, on average.

[1]*Alle alle*
[2]*Cepphus carbo*
[3]*Cepphus grylle*
[4]*Cepphus columba*
[5]*Brachyramphus brevirostris*
[6]*Brachyramphus marmoratus*
[7]*Aethia cristatella*
[8]*Aethia pusilla*
[9]*Aethia pygmaea*
[10]*Ptychoramphus aleuticus*
[11]*Cyclorrhynchus psittacula*
[12]*Cerorhinca monocerata*
[13]*Fratercula cirrhata*
[14]*Fratercula corniculata*
[15]*Fratercula arctica*

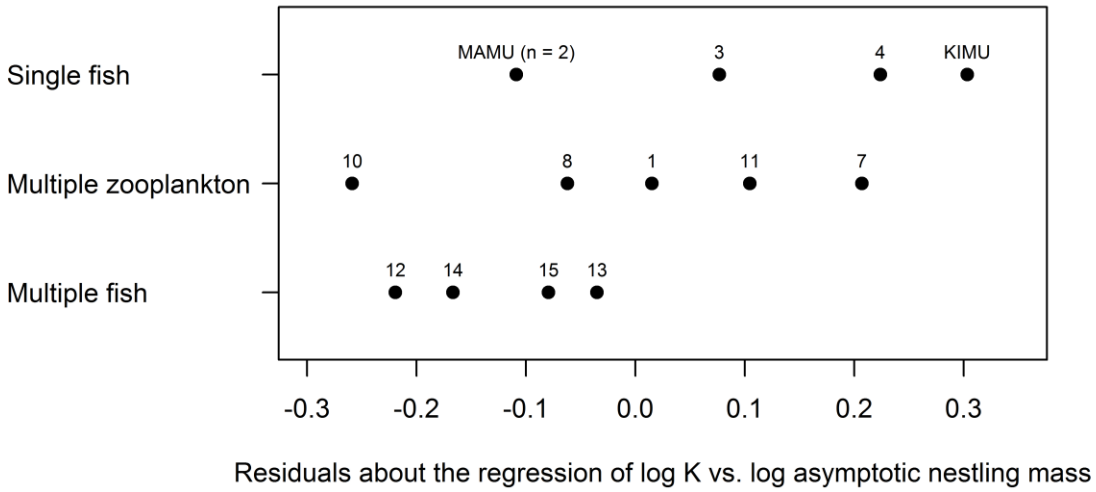

Figure 2.8. Distribution of residuals from an allometric regression of log mean logistic growth rate constant (K) against log mean nestling asymptotic body mass for 13 species of semi-precocial alcids, segregated by parental provisioning strategy (data from Table 2.7).

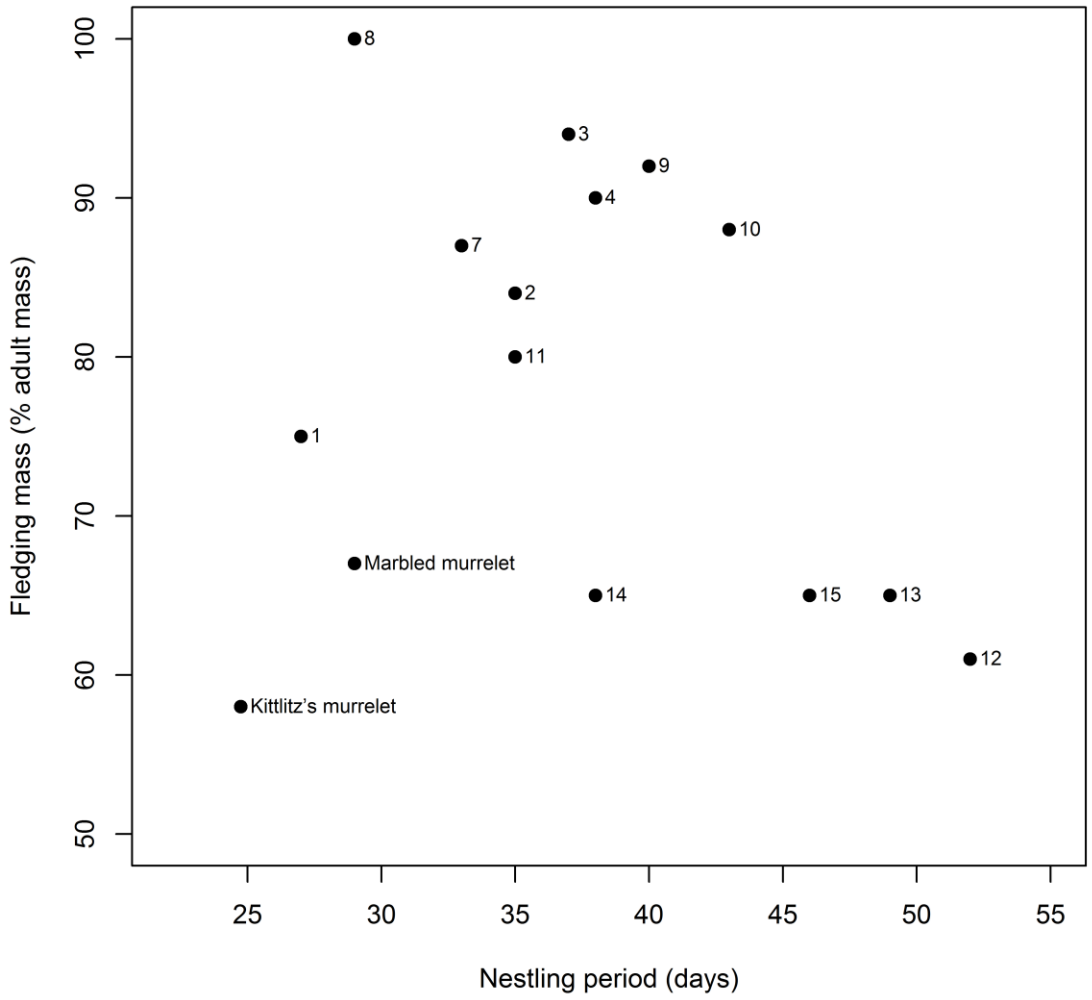

Figure 2.9. Average fledging mass (% of adult mass) as a function of mean nestling period (days) for 15 species of semi-precocial alcids (after Ydenberg 1989; data from Table 2.7).

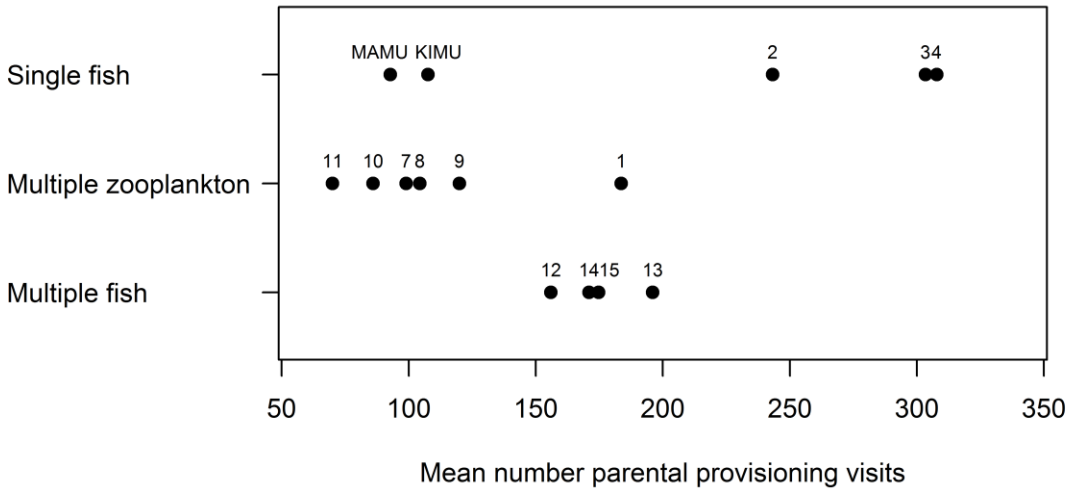

Figure 2.10. Mean number of provisioning visits required for successful fledging of chicks for 14 species of semi-precocial alcids, segregated by parental provisioning strategy. Provisioning rates for *Cepphus* species based on a brood size of one chick (data from Table 2.7).

CHAPTER 3

NEST SITE SELECTION BY KITTLITZ'S MURRELETS ON KODIAK ISLAND, ALASKA

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ABSTRACT

We studied aspects of nest site selection by Kittlitz's murrelets (*Brachyramphus brevirostris*) in an unglaciated area on Kodiak Island, Alaska during the 2008-2011 breeding seasons. We discovered 54 Kittlitz's murrelet nests on scree-dominated slopes between 188 and 454 m above sea level. Four nest sites were reused once in a subsequent study year, and 10 additional active nests were located within 60 m of an active nest site from a previous year of the study, suggesting fidelity to nest sites and nesting areas. Within years, discovered active nests were well dispersed across the landscape, with an average annual nest density of 0.0918 nests/ha of habitat searched. Nest scrapes were located on the surface of scree slopes with an average slope of 28.8° and mean vegetation coverage of 6.6%. Nests were usually situated immediately downslope from one or more large rocks. Using a variety of statistical approaches, we compared the habitat characteristics of nest sites at several scales with those of randomly selected sites without nests from throughout our searched area. Best-fit logistic regression models and random forest analysis indicated that areas within 5 m of nest sites were less vegetated, had more intermediate-sized rocks, and were located on steeper slopes. Univariate analysis indicated that areas within 25 m and 50 m of nests had significantly less vegetation cover and were located farther from vegetated edges. Univariate analyses also indicated that nest sites were significantly more likely to be on north-facing slopes. There was no evidence that nest sites differed from random plots in elevation, proximity to ridge-tops, or distance to the ocean. We did not find any evidence for differences in nest survival

rates associated with habitat covariates. The high dispersion of active nests and sparse vegetation in areas near nest sites, which appeared to support few alternative prey sources, suggest that nest site selection by Kittlitz's murrelets on Kodiak Island reflects a strategy to avoid encounters with nest predators.

INTRODUCTION

The Kittlitz's murrelet (*Brachyramphus brevirostris*) is a rare Beringian seabird in the family Alcidae, whose breeding ecology and nesting habitat are poorly-known. This species and the two congeneric species, the marbled murrelet (*B. marmoratus*) and long-billed murrelet *(B. perdix),* are unusual among seabirds in that they are non-colonial nesters, are cryptically colored during the breeding season, and appear to nest primarily inland in mainland habitats rather than on islands free of terrestrial predators (Gaston & Jones 1998). Very few nests of Kittlitz's murrelets have been described (Day et al. 1983; Day 1995; Piatt et al. 1999), and there are few data on nesting habitat selection for the species.

At-sea survey data suggest recent population declines for Kittlitz's murrelet, at least in some portions of its range (Kuletz et al. 2011a, 2011b; Piatt et al. 2011). These apparent declines, combined with a small global population largely restricted to a few areas during the breeding season and the species' suspected sensitivity to climate change (van Vliet 1993, Kuletz et al. 2003), have prompted concern about the status and conservation of the species (USFWS 2011). The extreme difficulty in locating Kittlitz's murrelet nests, however, has limited our understanding of those factors that influence the suitability of potential nesting habitat.

Limited data suggest that Kittlitz's murrelets have fairly specific habitat requirements for nesting. They appear to prefer nesting in remote areas, predominately among scree and talus located on mountain sides with slopes between 20^{o} and 45^{o} (Day et

al. 1999; Piatt et al. 1999). Adult Kittlitz's murrelets tend to aggregate at sea near tidewater glaciers and heavily glaciated terrain during the breeding season; consequently, nests are thought to often be associated with scree and talus habitats that are products of recent glacial action, although few nests have yet been described in such habitats (Day et al. 1999; Piatt et al. 1999). Consistent with the species' apparent preference for rocky mountain slopes, most previously described nests have been characterized by sparse vegetative cover near the nest site (Day et al. 1983, 1999). Nests have been discovered from 0 to 75 km inland from the coast, at elevations as high as 2000 m (Day et al. 1999), and appear to be widely dispersed across the landscape, with average nearest neighbor distances between nests of over 200 m (Kaler et al. 2009). It has been hypothesized that these characteristics reflect a strategy of predator avoidance in the face of high risks of nest predation associated with nesting in mainland habitats (Piatt et al. 1999).

The risk of nest predation for Kittlitz's murrelets might be considerably higher than for other alcids (excluding *Brachyramphus* alcids), which typically nest on small offshore islands or on steep sea cliffs, where terrestrial predators are absent or rarely able to access nest sites (Gaston & Jones 1998). Other attributes of Kittlitz's murrelet breeding ecology support the hypothesis that the risk of nest predation is a major selection pressure. Breeding adults are highly cryptic during the nesting period, and most parental visits to the nest occur during twilight periods at dusk and dawn, when avian predators are presumed to be least active (Sealy 1973). Compared to other alcids, parents visit their

nest sites infrequently, minimizing the risk of detection at the nest and/or interception of adults by land-based predators (Day et al. 1999; Chapter 2).

While general habitat associations have been described for scattered Kittlitz's murrelet nests found across mainland Alaska, the Aleutian Islands, and Beringian Russia, statistically rigorous, large-scale studies of nest site selection in the species have not yet been published, with the notable exception of Kaler et al. (2009); this study reported basic nest site selection characteristics for 11 Kittlitz's murrelet nests discovered on Agattu Island, Alaska, a small island in the western Aleutians where terrestrial predators are absent. In particular, nesting habitat has generally been described at the scale of the nest site itself, and has not been compared to unused areas of potential nesting habitat, although Kaler et al. (2009) did compare nest sites with plots located 50 m from each nest site.

The hypothesized strong selection pressure to avoid nest predation suggests that Kittlitz's murrelets would select nest sites that minimize the probability of detection by a nest predator. Nest predation risk has been shown to vary for many species of birds, depending on habitat characteristics surrounding the nest and across a range of spatial scales (Martin & Roper 1988; Møller 1989; Martin 1993). In particular, the size of patches of suitable habitat and the distance from habitat edges are often positively associated with nest survival (Angelstam 1986; Hoover et al. 1995; Keyser et al. 1998). The proximity of nest sites to habitat edges, the size of suitable habitat patches, and the

characteristics of habitat around the nest site may all be important factors for nest site selection in Kittlitz's murrelets and, *ipso facto*, important determinants of nest success.

Potential factors influencing the availability and quality of Kittlitz's murrelet nesting habitat include glacier recession due to climate change (Kuletz et al. 2003) and changes in the abundance and distribution of nest predators (USFWS 2011). Concern for the conservation of Kittlitz's murrelets in the face of these changes underscores the need for large-scale studies of Kittlitz's murrelet nest site selection. By identifying potential nesting habitat for Kittlitz's murrelets across the species' range, the impact of ongoing ecological change on the availability and distribution of suitable nesting habitat can be quantified.

To address this information need, we studied the nest site selection of Kittlitz's murrelets at a variety of spatial scales in Kodiak National Wildlife Refuge, Kodiak Island, Alaska, over four breeding seasons. Our primary objective was to determine the most informative predictors for the presence of an active Kittlitz's murrelet nest within the context of our overall hypothesis: that this species selects nest sites that tend to minimize the risk of nest predation in a landscape where terrestrial predators are present. We predicted that Kittlitz's murrelets would nest in areas with minimal vegetation cover and, moreover, would preferentially select nest sites located within larger patches of unvegetated terrain, and would avoid ecotones where non-vegetated patches meet vegetated terrain. We also predicted that the survival of Kittlitz's murrelet nests would be inversely related to percent vegetation cover and distance from habitat edges. To provide

much-needed information about general nest site characteristics, we also sought to collect detailed descriptive data about active nest sites.

METHODS

Study Area

Kodiak Island lies approximately 50 km southeast of mainland Alaska, and is by far the largest island in the Kodiak Archipelago, with a land area of 8,975 km^2. Mountains cover most of the interior of the island, with a major range extending southwest-northeast across the length of the island; several peaks exceed 1,200 m in elevation. The island's land cover is dominated by shrub, meadow, and dwarf shrub communities, with approximately 5% of the island's surface area consisting of bedrock outcrops and talus/scree (Fleming & Spencer 2007), ground cover types considered potentially suitable for nesting by Kittlitz's murrelets (Day et al. 1999). Most of this latter habitat type occurs above 600 m elevation.

We studied nest sites of Kittlitz's murrelets in the southwestern portion of the island during 2008 to 2011 (Figure 3.1). Our overall study area encompassed approximately 700 ha of scree/talus slopes and rock outcrops, which were distributed in discrete patches within a matrix of vegetated terrain. These patches of suitable nesting habitat ranged from 80 to 471 m elevation. The parent material in the study area is classified as ultramafic, a type of igneous rock containing high concentrations of heavy metals and scarce nutrients; this combination precludes the growth of most plants

(Alexander et al. 2007). These expanses of ultramafic rock resulted in sparsely-vegetated scree habitats within our overall study area that were at low elevations compared with similar habitats elsewhere on Kodiak Island. Contrastingly, herbaceous and woody vegetation dominated adjacent mountain slopes of comparable elevation where non-ultramafic bedrock occurred. Although Kittlitz's murrelets are usually associated with tidewater glaciers and glaciated terrain during the breeding season, the nearest glaciated terrain was approximately 70 km from the study area. Snow was almost completely absent from our study area during the peak of nest initiation in early June.

We conducted most of our research in the eastern-most portion of the study area during 2008, and expanded our study area to its full extent during 2009-2011 (Figure 3.1). All patches of habitat searched for nests were within ca. 5 to 11 km from the coast. Substrate size within patches of apparently suitable nesting habitat ranged from large outcrops of unbroken bedrock exceeding 10 m^2 to fine particles less than 1 cm in diameter. Average substrate size was generally small; approximately 70% of sampled rock substrate within the study areas was less than 10 cm in diameter. In general, scree slopes within the study area were very sparsely vegetated with a variety of widely dispersed sedges, forbs, and small prostrate shrubs, and occasional patches of vegetation greater than 2–5 m^2 in area. Scree slopes generally graded into larger patches of prostrate Sitka alder (*Alnus sitchensis*) and crowberry (*Empetrum nigrum*) at lower elevations and slopes, and at higher elevations at the edge of ultramafic exposures. Vegetation surrounding ultramafic exposures was dominated by upland and lowland tundra, mixed

forb meadows, and shrub communities composed of Sitka alder and willows (*Salix* spp.). No point within any of the scree slopes in our study area was more than 250 m from completely vegetated terrain.

We located Kittlitz's murrelet nests by systematically searching terrain dominated by scree, talus, and unbroken bedrock. Search efforts were concentrated in large patches of scree and talus, which were searched systematically so that large blocks of terrain were completely and contiguously covered. Two to five searchers walked 5–10 m apart and abreast of each other, generally following the slope contour from one edge of the scree slope to the other. Following the completion of each search transect, searchers moved perpendicular to the contour and repeated the search transect in the opposite direction until the entire slope had been searched. We placed pin flags during searches and used track functions on handheld GPS units to ensure that searches were conducted systematically and completely covered the potential habitat.

We searched areas for active murrelet nests in terrain that we presumed to be highly suitable (large patches of scree or talus at high elevation and high slopes, and with very sparse vegetation cover) as well as less suitable habitat (small patches of scree or talus, low elevation, low slope, moderate vegetation cover), based on characteristics of previously described nests in other areas of Alaska (Day et al. 1999, Kaler et al. 2009); we searched a range of potential nesting habitat in order to ensure accurate characterization of the habitat used by nesting Kittlitz's murrelets. Areas within 30–50 m of a known active nest were not searched to avoid disturbance to breeding adults. Nest-

searching extended from late May or early June to mid- or late July in all four years of the study. The primary round of nest-searching occurred over a broad search area during an approximately one-month period when the number of active nests was presumed to be at a peak. A second round of nest-searching covered a less expansive search area and lasted two to three weeks. All but one active nest was discovered when an incubating adult flushed from the nest. Adult Kittlitz's murrelets were identified upon flushing by their diagnostic white outer rectrices; in some cases we confirmed species identification using remote camera images or by viewing the incubating adult with a spotting scope, using culmen morphology as a distinguishing field mark (Day et al. 1999).

We collected data on nest site characteristics once nests were no longer active; most nesting habitat was assessed during late July to mid-August. We treated nest scrapes reused in subsequent study years as separate nests for analysis. We measured nest dimensions and classified the type and composition of substrate in and immediately surrounding the nest scrape. Slope aspect at the nest site was recorded, and average slope for a 10-m strip extending through the nest down the fall line was measured using a clinometer. Nest site location was recorded with a handheld GPS (Garmin 76 CSx) and elevation of the resulting waypoints was derived from a raster-based digital elevation model with a 10-m resolution in ArcGIS 10. Ocean visibility was determined from a standing position at the nest site and assigned to categories of either visible or not visible.

To address the influence of ground cover composition on nest site selection at different scales, we assessed habitat characteristics within three concentric circular plots

with radii of 5 m, 25 m, and 50 m, centered on each nest site. In the 5-m radius plot, we visually estimated proportional coverage values for 13 different classes of ground cover, as well as total percent vegetation cover (not including lichens). In the 25-m and 50-m radius plots, we estimated only total percent vegetation cover (not including lichens). At larger scales, we used ArcGIS 10 to determine the location of each nest site relative to landscape features. Because elevation varied among the ridge tops and mountain peaks in our study area, we measured the distance of the nest from the highest point immediately upslope on the fall line in order to standardize measurements of distance to ridge top. To measure distance of a nest from an ecotone, we calculated the distance from each nest to the nearest patch of vegetation (> 50% vegetation cover) greater than 0.5 ha in area using high-resolution ortho photography images. We also calculated the shortest straight-line distance of the nest site from the sea.

To identify the habitat characteristics of searched areas that were not used by nesting Kittlitz's murrelets, we randomly selected non-nest plots at two different spatial scales. First, we located two "near-nest" plots at a random bearing and distance (between 50 and 150 m) from each active nest site, and surveyed these plots in the same manner as nest plots. The center of any given near-nest plot was constrained to fall within the area searched for nests during that breeding season, and was located at least 50 m from the other near-nest plot for any given nest. We used a spinner to generate random numbers to determine bearing and distance to near-nest plots and used hand-held GPS units to confirm that near-nest plots fell within our searched area.

Second, to identify nest site characteristics relative to available habitat on a broader spatial scale, we surveyed a total of 449 non-nest plots that were randomly located within the entire area searched during each nesting season. We located and surveyed these random plots in each year of the study in order to compensate for slight inter-annual differences in the area searched for nests; by doing this we ensured that random plots could fall throughout the searched terrain in any given year. Random plots were constrained to fall at least 50 m from each other, and at least 25 m from any active nest found during that breeding season. To ensure representative sampling effort across all searched habitats, we constrained the number of random plots sampled in each area of potential nesting habitat (see Figure 3.1) to be proportional to the total area searched within each of these ultramafic search areas in each study year. We used a random point generating feature in ArcView 3.3 to determine the location of random points within searched terrain during each year. Potential bias in estimation of habitat variables among years was minimized by thorough training of field research assistants by the same field crew leader in all four years of the study.

Data Analysis

We performed analysis of variance (ANOVA) to test for differences in the means among the three plot types (nest, near-nest, and random) for 22 habitat covariates, using appropriate transformations to meet assumptions of normality and equal variance, when necessary. For covariates with significant differences ($\alpha = 0.05$) among groups, we compared nest plots to near nest plots and to random plots using *t*-tests. To minimize the

possibility of type II errors, we did not adjust α to compensate for multiple comparisons (Rothman 1990; Gotelli & Ellison 2004). We tested for patterns in nest site aspect by assigning aspect to one of the four cardinal directions and creating a logistic regression model that compared the aspect of nest plots against that of random plots. For model selection, we considered plot aspect as either north- or south-facing to avoid confounding aspect with our ocean view variable. To reduce the number of possible habitat variables for eventual model selection, we dropped covariates from further analysis that displayed *P*-values > 0.35 for ANOVAs; however, we initially retained all covariates related to ground cover for further investigation with the exception of soil cover, which comprised only a trivial proportion of total ground cover for all plot types.

We performed principle components analysis (PCA; Johnson 1998) using the program PCord to explore ground cover data and reduce the number of ground cover covariates entered into our model selection procedure, and to create orthogonal principle component (PC) axes for correlated ground cover covariates for use in initial model selection. We used PCA based on the correlation matrix for data exploration and reduction in order to account for wide variation in the scale of covariates, and used PCA based on the covariance matrix for creating PC axes for use in model selection.

We used logistic regression to determine differences in habitat characteristics among nest, near-nest, and random plots (Hosmer & Lemeshow 2000). We initially performed logistic regression on retained covariates and orthogonal PC axes that accounted for ground cover. We then substituted ground cover covariates suggested by

significant PC axes in our initial logistic regression model, along with all other retained covariates, into a final global logistic regression model. For logistic regression model selection, we used a best subsets procedure that uses Akaike's Information Criterion (AIC; Burnham & Anderson 2002) to determine the most parsimonious models using the "bestglm" package in R. We assessed potential multi-collinearity of our predictors by calculating variance inflation factors (VIFs) for all covariates in our global models before model selection, and used a value of 10 as a cut-off for potential inclusion in models (Kutner et al. 2004). We assessed goodness-of-fit of our final models using the Hosmer-Lemeshow goodness-of-fit test (Hosmer & Lemeshow 2000). We used Wald's test and associated *P*-values to determine the significance of predictors.

Because we suspected potential non-linear relationships among predictors and because ground cover covariates included in our logistic regression models comprised portions of a linear combination, we used random forests analysis (hereafter RF) to verify and rank the importance of predictors suggested by our logistic regression models. RF is a recursive partitioning technique that involves an ensemble of classification trees where each split in a tree is based on a random sample of predictors (Breiman 2001). RF analysis is similar to classification and regression trees (CART). It can account for non-linearity of predictor variables, and makes no assumptions about normality, independence, or homoscedasticity, but is more robust to small differences in the data and can better account for potential multi-collinearity among predictors (Breiman 2001; Cutler et al. 2007; Strobl et al. 2008).

We conducted RF analysis using R's "party" package, and used an unbiased tree algorithm to generate conditional variable importance scores. Because our data were unbalanced for all comparisons, we created RFs based on subsets of the larger sample group. Because exploratory RFs proved somewhat unstable to differences in subsets drawn for model training, we generated 100 unique RFs for each plot comparison. Each RF contained 500 trees based on a different training subset; each split in a given tree was based on four randomly-permuted predictors. We averaged scaled conditional importance scores across all RFs to assess the overall influence of predictors across all subsets of data. We followed the recommendation by Strobl et al. (2009) and interpreted variable importance measures only as a descriptive ranking of the influence of predictors on classification. We included all retained covariates in the RF analysis, with the exception of percent vegetation cover, for which we only included percent vegetation cover at the 25-m radius scale. We used percent vegetation cover at the 25-m scale for RF analysis, instead of at the 5-m scale, as a precaution to avoid biases related to potential collinearity with other ground cover covariates in the analysis.

We used Program MARK to determine whether habitat variables had any influence on daily nest survival rates for Kittlitz's murrelet nests. Program MARK incorporates a maximum likelihood approach for calculation of nest survival rates and is useful for determining the influence of habitat covariates on nest survival (Rotella et al. 2004). We incorporated four habitat covariates suggested by our nest site selection analyses into models that assumed constant nest survival and evaluated candidate models

using AICc. We created a confidence set of models by excluding models with AICc weights that were less than 10% of the top model (Burnham & Anderson 2002). We used methods outlined in Burnham and Anderson (2002) to average coefficient estimates for models in our confidence set.

RESULTS

Nest characteristics and spatial distribution

We discovered a total of 53 active Kittlitz's murrelet nests during the 2008-2011 breeding seasons (2008, n = 4; 2009, n = 12; 2010, n = 15; 2011, n = 22), plus one inactive nest in 2010 that contained a chick that had recently died. Because of the limited sample size of active nests found in any given year and in each of the four search areas comprising the overall study area, we pooled nests from all years and search areas for analysis. All nests were located in areas dominated by scree, with an average percent cover of 93.3% (SD = 6.9, range = 67–99%, n = 54 nests) unvegetated rock substrate within 5 m of the nest. Only one nest was located within 100 m of a patch of snow.

Nest scrapes were generally circular to slightly ovoid, with a mean diameter of 14.0 cm (SD = 1.58, range = 9.5–20.0 cm) and depth of 2.7 cm (SD = 1.02, range = 0–5.0 cm). The substrate of the nest scrape itself consisted mostly of rock < 1 cm in diameter (mean = 55.0% cover, SD = 29.7, range = 0–95%) and rock 1–5 cm in diameter (mean = 41.0% cover, SD = 28.9, range = 0–98%), with a higher proportion of rocks in the larger size class at the margin of the nest scrape (< 1 cm rock = 32.9% cover, SD = 21.1, range

= 0–80%; 1–5 cm rock = 54.2% cover, SD = 23.7, range = 0–100%). In three cases the nest scrape consisted almost entirely of a patch of moss, and some moss cover was commonly found at the margins of active nests.

All nests had at least one relatively large rock or, in two cases, a combination of a large rock and a large moss cushion, situated immediately upslope of the nest scrape; these upslope features were generally of sufficient size to obscure the incubating adult murrelet from the view of an upslope observer. The average size of this upslope feature was 28.3 cm in its largest dimension (SD = 9.6, range = 10–63 cm). However, these features were usually not the largest feature within a 5-m radius of the nest scrape. In some cases several large rocks surrounded the nest scrape on the upslope side, and presumably provided the nest some degree of protection from high winds and precipitation, and possibly provided concealment or protection from potential predators.

Four different nest scrapes were reused once during a subsequent year of the study, but no nest scrape was reused within the same breeding season. An additional 10 active nest scrapes were located less than 60 m from a nest scrape active in a previous year. Thus, a total of 28 out of 54 nests (ca. 52%) were located within 60 m of an active nest found during a different year of the four-year study. Furthermore, five murrelet nest scrapes that had apparently been used in previous years were discovered less than 15 m from four different active murrelet nests. These inactive nest scrapes contained decomposing egg shell fragments, often buried beneath moss or gravel, indicating that the nest scrape had not been used earlier in the current breeding season.

Active nests were generally widely dispersed across the landscape, with a median within-year nearest neighbor distance of 344 m (range = 13–1,550 m); however, 9 of 53 active nests (17%) were less than 100 m from another concurrently active nest. One active nest was less than 100 m from two concurrently active nests. Two concurrently active nests were separated by only 13 m, and another pair was separated by only 46 m; there was no visual barrier between nests for either of these pairs, and presumably parent birds were aware of the close proximity of their neighbors.

The mean density of active nests discovered during 2009-2011 was 0.0918 nests/ha of searched terrain (SD = 0.0237, range = 0.0717–0.118, n = 3 years). We did not include 2008 data in this estimate because our nest search was limited to a much smaller area during that year, and we searched a much higher proportion of partially-vegetated terrain than in the subsequent three years. While we believe that we detected the vast majority of active nests within the areas searched, this estimate of nest density is nevertheless biased low because it does not include nests that failed before the area in which they were located was searched.

Nest site selection

Significant differences in 12 habitat variables were found between nest plots, near-nest plots, and random plots, as indicated by *t*-tests (Table 3.1). There was no evidence that Kittlitz's murrelets selected nest sites within the areas searched for nests that were (1) closer to the ocean, (2) closer to a ridge top, or (3) higher in elevation above sea level. Logistic regression analysis indicated that nests were significantly more likely

to be located on north-facing slopes ($P = 0.02$) and less likely on south-facing slopes ($P = 0.04$) compared to random plots. The percentage of total nests on slopes of various aspects was: 48% north, 17% east, 9% south, and 26% west, while the percentage of random plots with respect to slope aspect was 32% north, 16% east, 21% south, and 31% west.

Exploratory PCA suggested strong correlations among some habitat covariates, and potential surrogates for highly correlated covariates. PC axes 1 and 2 accounted for 58% of the total variation among ground cover covariates at the scale of 5-m radius plots. Vectors of covariates in ordination space indicated that the percent cover of all classes of vegetation (except lichens) loaded similarly on PC axes 1 and 2 at the 5-m radius scale (Figure 3.2), so we used percent cover of total vegetation at the 5-m scale as a surrogate for percent cover of each vegetation class in subsequent analyses. We treated percent cover of lichens as a separate covariate in later analyses because this variable did not load similarly to percent cover of vegetation or percent cover of various rock size classes. Total percent cover of vegetation at the 5-m, 25-m, and 50-m scales loaded similarly (Figure 3.2) and provided somewhat redundant information because percent cover of vegetation at the smaller plot size would necessarily be included in larger plots; therefore, we used percent cover of vegetation at the 5-m scale as a surrogate for percent cover of vegetation at both larger scales for logistic regression analysis. The percent cover of rocks > 20 cm in diameter and the percent cover of rocks > 30 cm in diameter loaded

similarly in the PCA and provided redundant information, so we dropped percent cover of rocks > 20 cm in diameter from all further analyses (Figure 3.2).

In our final PCA on ground cover covariates (retained and surrogate), PC axes 1 and 2 accounted for the vast majority of cumulative variance for 5-m radius plots (78.4%, Table 3.2). Axis 1 showed high positive loading for percent cover of vegetation and negative loading for percent cover of rock size classes from < 1 cm to 30 cm in diameter (Table 3.2). Loadings from axis 2 represented a rough contrast between percent cover of larger rock size classes (5 cm to 30 cm) vs. percent cover of rocks < 5 cm and vegetation (Table 3.2). PC axis 3 represented a strong contrast between percent cover of intermediate-sized rocks and percent cover of large rocks > 30 cm in diameter (Table 3.2). Together, PC axes 1-3 accounted for 90.9% of cumulative variance for 5-m radius plots (Table 3.2). When considering a plot of the first two PC axes, a dense cluster of points from all three plot types was concentrated at negative values on the PC 1 axis, indicating low percent cover of vegetation for most plots of all three types, while the relatively evenly dispersed points of all three plot types along the PC 2 axis indicate no clear distinction among plot types for this PC axis (Figure 3.3). Convex hulls for the three plot types indicated that nests occupied a much smaller area in ordination space than did near-nest or random plots.

Initial logistic regression analyses indicated that PC axes 1 and 3 were significantly different between nest plots and both random (PC 1, $P = 0.007$; PC 3, $P < 0.001$) and near-nest plots (PC 1, $P = 0.007$; PC 3, $P < 0.001$), but there was no

difference in ground cover covariates between near-nest and random plots. For our final models, we substituted percent vegetation cover at the 5-m radius scale for PC 1 and percent cover of rocks 5–10 cm, 10–30 cm, and > 30 cm at the 5-m radius scale for PC 3. Nest plots were significantly more likely to have greater slopes ($P < 0.001$ and $P = 0.003$, respectively), greater percent cover of rocks 10–30 cm in diameter ($P < 0.001$, $P = 0.001$), lower percent cover of vegetation ($P = 0.02$, $P = 0.04$), and lower percent coverage of rocks > 30 cm ($P = 0.02$, $P = 0.01$) compared to random plots or near-nest plots (Table 3.3). Near-nest plots were not significantly different in ground cover from random plots, but were significantly more likely to have greater slopes than random plots.

Because our ground cover covariates comprised a portion of a linear combination (i.e., a change in one covariate would likely cause changes in others), we investigated the sensitivity of our final models to the addition of percent cover of rocks 5–10 cm, which was suggested by univariate analysis and PCA to be a strong predictor of nest sites. The coefficient estimates for percent cover of rock size class 5–10 cm and rock size class > 30 cm were highly unstable when both covariates were included in a logistic regression model, indicating significant multicollinearity. We thus relied on the RF analysis to clarify the importance of percent cover of rock size class 5–10 cm.

Variable importance rankings from the RF analysis indicated that most of the significant predictors in our final logistic models were the most important determinants of plot classification for the RFs (Table 3.4). The one exception was percent cover of rock size class 5–10 cm, which was the third most important variable for distinguishing nest

plots from random plots in the RF analysis. Percent cover of rock size class 10–30 cm was the most important variable for discriminating between nest plots and both random plots and near-nest plots, while slope was the most important variable for discriminating between near-nest plots and random plots.

Nest survival

Covariates entered into our nest survival models included (1) percent cover of rock size class 10–30 cm, (2) slope, and (3) percent cover of vegetation within 25 m of the nest. Although not indicated by our model selection procedures, we also included as a habitat covariate (4) nearest distance to a vegetated edge, because proximity to edge is known to be a source of reduced nest survival for many ground-nesting birds (Angelstam 1986; Keyser et al. 1998).

We tested all possible permutations of the habitat covariates for our nest survival analysis (n = 16), including a constant survival model without habitat covariates (Mayfield estimate). Our confidence set included 15 models with AIC weights within 10% of the weight of the top model; all models in the confidence set were within 3.5 AIC points of the top model. We averaged parameter estimates among our confidence set using methods outlined in Burnham and Anderson (2002). Confidence intervals (95%) for model averaged parameter estimates all overlapped zero, indicating no significant influence of habitat covariates on nest survival rate.

DISCUSSION

Spatial distribution of nests

Although we had no means of identifying individual murrelets, the reuse of nest sites, the close proximity of a large subset of nests to previous nest sites, and the proximity of apparent previously-used nest sites to active nests suggest fidelity of breeding Kittlitz's murrelets to nest sites and nesting areas. This is consistent with limited information for Kittlitz's murrelet (Piatt et al. 1999) and marbled murrelet (De Santo & Nelson 1995; Hébert & Golightly 2006; Barbaree 2011), and the well-documented nest area fidelity for other alcid species (De Santo & Nelson 1995). Consistent with the literature (Day et al. 1999; Kaler et al. 2009), we found that Kittlitz's murrelets generally nested in a dispersed manner across the landscape during any breeding season. This apparent dispersion of active nests may be an adaptation to reduce the probability of detection by predators. It has been hypothesized that potential predators are less efficient at locating prey that are widely spaced (Tinbergen et al. 1967), and that an organism's concealment from predators is maximized under conditions where its probability of occurrence in a given habitat is low (Merilaita et al. 1999).

Nest site selection

At the smallest scale of our nest site selection analyses (5-m), nest plots had a lower percent cover of vegetation, higher percent cover of rocks 5–30 cm in diameter, lower percent cover of rocks > 30 cm in diameter, and higher slope angles compared to random plots and near-nest plots. Logistic regression models suggested that low

vegetation cover within 5 m of the nest was a significant driver in nest site selection. RF analysis indicated, however, that the importance of vegetation cover as a predictor ranked far below slope and percent cover of rocks 5–30 cm in diameter. The lower importance of vegetation cover in the RF analysis likely reflects a non-linear response of nest site preference relative to percent vegetation cover, which would not have been detectible with a linear logistic regression model. This interpretation is supported by the pattern of points in ordination space from PCA. Points representing plots of all types were highly clumped in regions of ordination space that corresponded to low vegetation cover, while only near-nest and random plots were located in areas that corresponded to higher vegetation cover (Figure 3.3). This suggests that below a certain threshold, vegetation cover was not a significant predictor of plot type. Thus, we concluded that percent vegetation cover in our study area significantly affected nest site choice, but other factors were more important once percent vegetation cover was below a threshold level.

The significant differences between nest plots and non-nest plots in percent vegetation cover at both the 25-m and 50-m radius plot scales suggest that selection for low vegetation coverage extended well beyond the nest site itself (Table 3.1). This suggests that Kittlitz's murrelets selected for relatively large patches with low percent vegetation cover, at least 50 m from the nest site. While the mean percent vegetation cover was consecutively higher at the 5-m, 25-m, and 50-m radius scales for nest sites, suggesting that vegetation cover was lowest at the microsite (5-m) scale, the same trend is apparent for non-nest sites (Table 3.1). These patterns are consistent with the landscape

of our study area and the nature of our search effort. Patches of sparsely vegetated terrain were relatively small, and about 80% of the area searched for nests was less than 100 m from the nearest vegetated edge. Because we concentrated our nest searches on sparsely vegetated terrain, the center of all three types of plots was usually very low in vegetation cover, but the probability of a plot being within 50 m of a vegetated edge was relatively high. Consequently, the increasing percent vegetation cover at larger plot sizes likely reflects the increasing probability of a plot including an area with 100% vegetation cover.

While the habitat characteristics of nest sites appear to be significantly different from random sites at both the small and meso scales (5 m to 50 m from the nest site), there was also some indication that habitat characteristics more than 50 m from the nest were different from those of randomly located sites. Consistent with our prediction, nest sites were significantly farther from vegetated edges compared to non-nest sites (Table 3.1). Near-nest sites were also significantly steeper than random sites, suggesting that large areas of steep slopes were preferred for nesting. Contrary to our predictions, however, there were no significant differences in percent vegetation cover between near-nest plots and random plots, suggesting that patch size, as it relates to a low percent vegetation cover, did not extend to 50–150 m from nest sites, where near-nest plots were located.

Because the contiguously searched regions of our study area were relatively few and discrete patches of sparsely vegetated habitat were generally similar in size, we were unable to address questions relating to patch size at large scales (> 150 m from nest sites).

However, it seems likely that size of patches of habitat suitable for nesting may be an important predictor of Kittlitz's murrelet nest site selection in other nesting areas, as it is with other species of ground-nesting birds (Davis & Brittingham 2004; Winter et al. 2006). Similarly, all searched habitats were relatively close to the nearest coastline– between 4.8 and 11 km–likely precluding our ability to detect the potential effects of distance to the ocean on nest site selection. Given the apparent high energetic costs related to parental meal deliveries to chicks (Hatch 2011), however, it seems likely that nesting habitat situated closer to at-sea foraging habitat would be preferred over habitats located far inland.

Comparisons with previously described nests

Nest habitats within our study area were generally similar to those described elsewhere (Day et al. 1983; Day 1995; Piatt et al. 1999), although some important differences were observed. Contrary to Day et al. (1999), where more than half of nests described were on south- or east-facing slopes, nests in our study were significantly more likely to be situated primarily on north- and west-facing slopes compared to random plots. Day et al. (1999) hypothesized that the orientation of nests may be related to increased habitat availability resulting from rapid snow melt on south-facing slopes; however, this factor would not apply to our study area because almost no snow was present when nesting was initiated. The nearest straight-line distance to the ocean was located to the west or northwest of all searched areas, which was consistent with the slope

aspect of most nests. Thus, nest orientation in our study area may have reflected a tendency for Kittlitz's murrelets to situate their nests on slopes that face the ocean.

The elevation of murrelet nests in our study area was considerably lower than that of most nests described from the southern portion of the species' range, where nests have been found up to 2,000 m (Day et al. 1999). The only nest found on Kodiak Island prior to this study was located at 901 m elevation (Stenhouse et al. 2008), nearly twice the elevation of the highest nest found during the present study. Additionally, most potential nesting habitat for Kittlitz's murrelets on Kodiak Island occurs at much greater elevations than are available within our study area (Stenhouse et al. 2008), suggesting that most nests elsewhere on Kodiak Island are at higher elevations than nests found within the study area. Similarly, our study area did not include any areas of glaciers or permanent snow, nor did it include extremely steep (> 45 degrees) terrain. The breeding distribution of Kittlitz's murrelet, however, is clumped in several regions where such steep, high elevation terrain is prevalent near the coast. Nests have been described in patches of scree surrounded by permanent snow and glacial ice, and on cliff faces (Day et al. 1983), and nests are suspected to occur on nunataks and in close proximity to glaciers in many areas of the species' breeding range (Day et al. 1999). It is possible, therefore, that our models for nest site selection on Kodiak Island are not wholly reflective of Kittlitz's murrelet nest site selection globally because of the relatively narrow range of potential nesting habitats available for Kittlitz's murrelets within our study area.

Along with most previously documented nests, nests within our study site were located in areas dominated by scree, with very little vegetation present near the nest scrape. This is in contrast with nests described from Agattu Island in the western Aleutians, where average vegetation cover at the nest site was 51% (Kaler et al. 2009). A further difference in nest site characteristics between Agattu Island and Kodiak Island was the composition of ground cover within 5 m of the nest scrape. While Kaler et al. (2009) reported the presence of orange crustose lichens and bare ground as being the best predictors of nest site presence within potential nesting habitats, neither of these factors were significant predictors on Kodiak Island. A potential explanation for differences between nest site characteristics on Agattu Island and Kodiak Island is the major difference in potential nest predators: Agattu Island is free of terrestrial mammalian predators, while terrestrial predators are abundant on Kodiak Island. Red foxes (*Vulpes vulpes*) were the most common mammalian predator within our study area, and were observed frequently in vegetated lowland areas adjacent to murrelet nesting habitat, but infrequently observed in scree-dominated habitats. Moreover, we observed very little potential prey for mammalian predators in poorly-vegetated searched terrain, with the exception of Kittlitz's murrelets. Thus, in the presence of terrestrial predators, Kittlitz's murrelets may select nest sites with a high proportion of rock cover and a concomitantly low proportion of vegetation cover, possibly because these areas would be less attractive to searching predators because of the scarcity of alternative prey.

Nest Survival

While we did not find a relationship between habitat covariates and nest survival rate, our limited sample size of nests may have precluded discovery of such an effect, if present. Moreover, only ca. 58% of unsuccessful nests failed due to depredation, with the remainder failing due either to chick death on the nest or parental abandonment of the egg (see Chapter 2). While risk of nest predation might be influenced by nest site characteristics, chick death and nest abandonment could be independent of nesting habitat. If this is the case, then potential habitat factors that influence nest predation rates may have been obscured by the large proportion of nests that failed for other reasons.

Nest success rates within our study area were very low during 2008-2011; only ca. 17% of discovered nests resulted in a fledged chick (Chapter 2). It seems likely that the low nest survival rate was related to the small size of patches of available nesting habitat, and to the presence and relative abundance of mammalian predators, such as red fox, in the study area. Our study area was characterized by relatively small "islands" of sparsely vegetated scree slopes surrounded by vegetated lowlands, and often interconnected to densely vegetated mountains. If the apparent selection for nesting habitats with low vegetation cover reflects a predator avoidance strategy, then it is possible that few nest sites within our study area were located far enough from vegetation to appreciably reduce depredation rates compared to nests located closer to vegetated edges. Similarly, the preponderance of vegetated matrix habitats surrounding suitable murrelet nesting habitat in the study area supported commonly observed red fox, which might have led to a high rate of predator encounters with murrelet nests that was

relatively independent of habitat characteristics. Terrestrial predator densities and the frequency of predator encounters with nests may be lower where murrelet nesting occurs in areas surrounded by snow, glacial ice, and extensive bedrock, talus, and scree, as is presumed to be the case for most Kittlitz's murrelet nesting habitat in Alaska (Day et al. 1999; USFWS 2011), including high elevation regions of Kodiak Island (Stenhouse et al. 2008).

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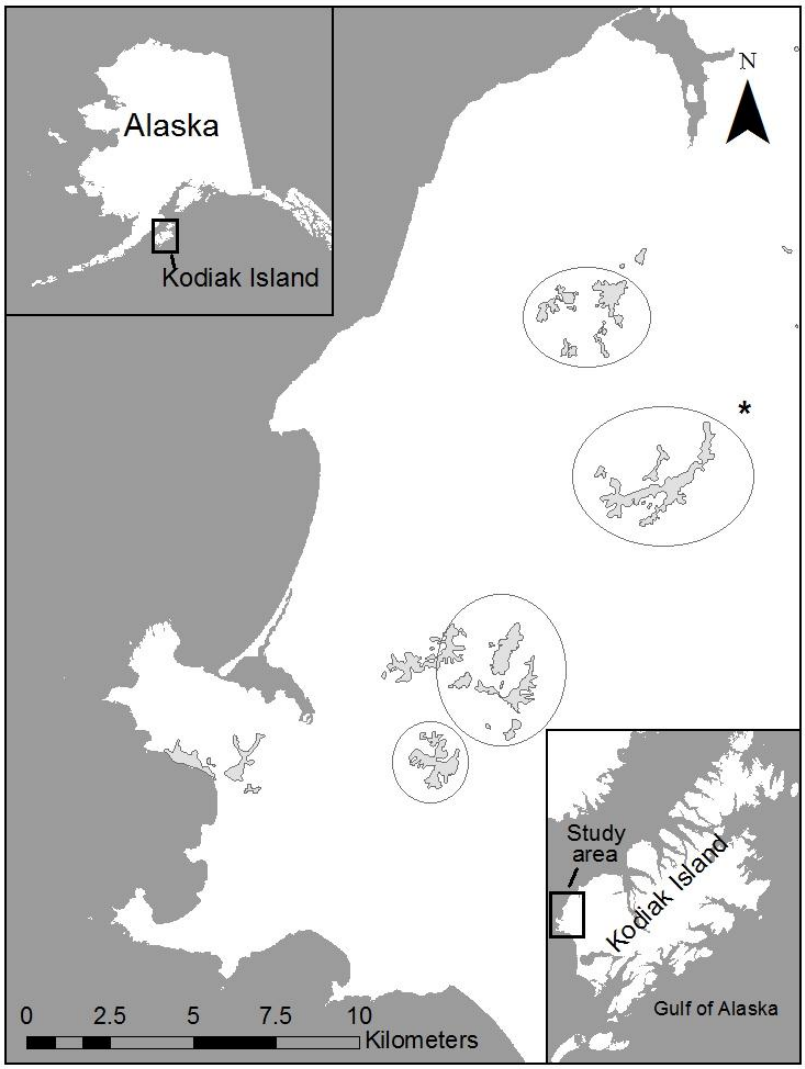

Figure 3.1. Map of the overall study area on Kodiak Island, Alaska. Light gray areas represent potential Kittlitz's murrelet nesting habitat dominated by scree, talus, and unbroken bedrock. Ovals encompass areas of potential nesting habitat that were systematically searched for Kittlitz's murrelet nests during 2009-2011. Asterisk indicates nesting habitat systematically searched during 2008-2011.

Table 3.1. Comparison of habitat variables among three plot types surveyed for Kittlitz's murrelet nests on Kodiak Island, Alaska during 2008-2011: (1) plots centered on a Kittlitz's murrelet nest site (nest plots), (2) plots centered on randomly selected points 50-150 m from a nest site (near-nest plots), and (3) plots centered on randomly selected points within the area searched for Kittlitz's murrelet nests (random plots). Values are means of untransformed variables ± SD; range in parentheses. Bold values indicate a significant difference ($P < 0.05$) between nest plots and either near-nest plots or random plots. Values denoted with "+" indicate $P < 0.01$, and "++" indicates $P < 0.001$.

Habitat variable	Nest plots (n = 54)	Near-nest plots (n = 100)	Random plots (n = 449)
Distance to open ocean (km)*	7.4 ± 1.5 (5.0-10.7)	7.4 ± 1.5 (5.0-10.7)	7.5 ± 1.7 (4.9-11.1)
Distance to vegetation edge (m)	79 ± 44 (8 - 215)	**64 ± 42** (1-177)	**63 ± 44** (0 - 221)
Distance to ridge top (m)*	95 ± 95 (6-409)	107 ± 98 (3-388)	104 ± 106 (1-624)
Ocean in view of plot (1 = Y)	0.85 ± 0.36 (0-1)	0.77 ± 0.42 (0-1)	**0.70 ± 0.46**$^{+}$ (0-1)
Slope	28.8 ± 4.0 (20-37)	**26.7 ± 5.3**$^{+}$ (7-45)	**25.1 ± 6.2**$^{++}$ (0-45)
Elevation (m)	325 ± 71 (188-454)	317 ± 65 (191-450)	307 ± 73 (157-463)
5-m radius % cover			
Rock < 1 cm	14.3 ± 7.6 (1-33)	16.0 ± 9.5 (1-50)	16.0 ± 9.8 (0-50)
Rock 1-5 cm	25.6 ± 10.0 (4-50)	26.1 ± 12.6 (1-59)	23.9 ± 12.4 (0-64)
Rock 5-10 cm	23.4 ± 6.2 (10-41)	**18.6 ± 10.3**$^{++}$ (4-70)	**18.1 ± 8.9**$^{++}$ (0-50)
Rock 10-30 cm	21.5 ± 10.6 (5-60)	**14.4 ± 8.3**$^{++}$ (2-40)	**14.4 ± 8.8**$^{++}$ (0-45)
Rock > 20 cm*	19.3 ± 10.7 (5-50)	17.4 ± 12.6 (0-55)	**16.3 ± 13.4** (0-81)
Rock > 30 cm	8.7 ± 6.9 (0-40)	11.4 ± 11.0 (0-45)	11.0 ± 12.6 (0-95)
Soil*	0.3 ± 0.6 (0-2)	0.3 ± 0.7 (0-4)	0.4 ± 0.9 (0-8)
Lichens	0.6 ± 1.1 (0-5)	1.0 ± 3.2 (0-30)	1.0 ± 2.4 (0-30)
Orange crustose lichens	0.1 ± 0.4 (0-2)	0.4 ± 1.6 (0-15)	0.3 ± 1.0 (0-10)
Moss*	2.0 ± 2.4 (0-10)	3.6 ± 6.0 (0-25)	4.4 ± 10.1 (0-90)

Table 3.1 (Continued)

Habitat variable	Nest plots (n = 54)	Near-nest plots (n = 100)	Random plots (n = 449)
Grass and sedge*	1.0 ± 1.0 (0-4)	**1.6 ± 1.8 (0-8)**	**1.9 ± 3.1++ (0-36)**
Forbs*	0.3 ± 0.4 (0-2)	**0.6 ± 1.0**$^{++}$ (0-5)	**0.8 ± 2.1**$^{++}$ (0-25)
Dwarf shrubs*	3.6 ± 5.5 (0-28)	**9.1 ± 15.0**$^{+}$ (0-79)	**11.8 ± 20.6**$^{++}$ (0-100)
Total vegetation	6.6 ± 7.0 (1-33)	**14.0 ± 18.1**$^{++}$ (0.1-89)	**16.3 ± 23.1**$^{++}$ (0-100)
% Vegetation cover (25-m radius)	9.0 ± 8.8 (0.1-45)	**17.0 ± 17.6**$^{++}$ (0-90)	**17.8 ± 20.7**$^{++}$ (0-99)
% Vegetation cover (50-m radius)*	11.5 ± 12.8 (0.1-70)	**18.1 ± 17.2**$^{+}$ (0-92)	**19.3 ± 20.5**$^{++}$ (0-92)

*Variables dropped from further analysis because of low *P*-values or collinearity

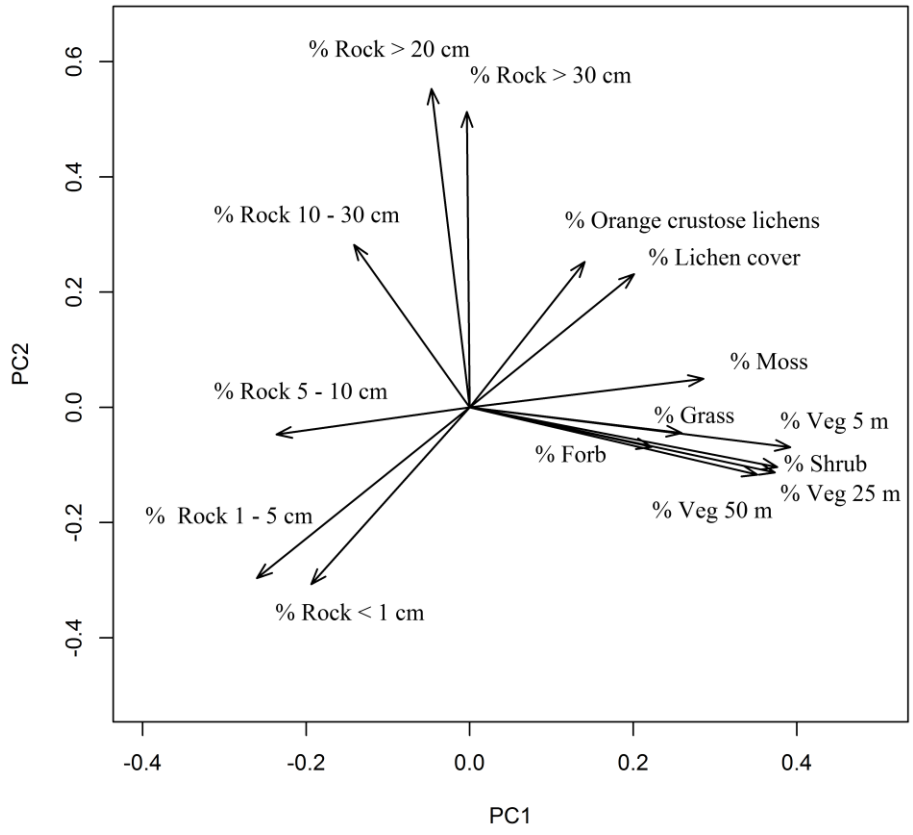

Figure 3.2. Vectors of ground cover covariates for principal component (PC) axes 1 and 2 from exploratory principal component analysis (PCA) for plots centered on Kittlitz's murrelet nests, plots randomly selected near murrelet nests, and plots randomly selected from the total area searched for murrelet nests on Kodiak Island, Alaska during 2008-2011. Angles between vectors of 0˚ or 180˚ represent correlations of 1 and -1, respectively.

Table 3.2. Axis loadings of covariates from principal component analysis (PCA) of ground cover habitat variables in 5-m radius plots (1) centered on a Kittlitz's murrelet nest, (2) within 50-150 m of a Kittlitz's murrelet nest, and (3) randomly selected from throughout the area searched for Kittlitz's murrelet nests on Kodiak Island, Alaska during 2008-2011. Per axis variance is presented in parentheses. Arrows represent axis loading sign and magnitude, axis loadings are in brackets.

Ground cover covariate	PC 1 (58.0%)	PC 2 (20.4%)	PC 3 (12.5%)
% Rock < 1 cm	↓ [-13]	↑ [22]	↓ [-19]
% Rock 1–5 cm	↓ [-23]	↑ [29]	↓ [-14]
% Rock 5–10 cm	↓ [-13]	– [-1]	↑↑ [32]
% Rock 10–30	– [-7]	↓ [-22]	↑↑ [33]
% Rock > 30 cm	– [1]	↓↓ [-44]	↓↓ [-35]
% Vegetation	↑↑ [55]	↑ [14]	– [2]

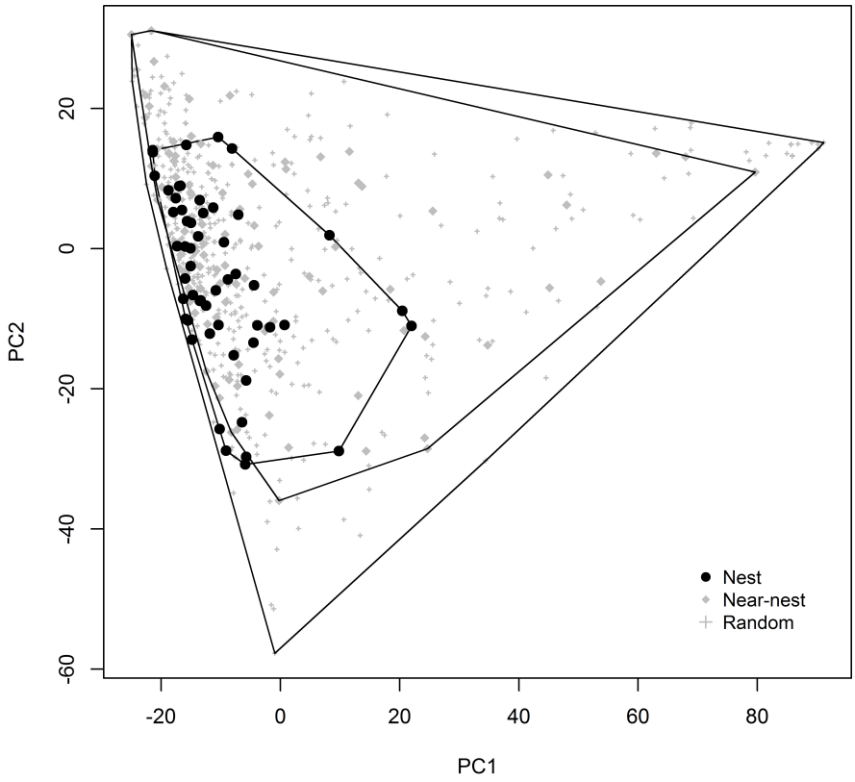

Figure 3.3. Ordination of plots along the first two principal component axes for ground cover in 5-m radius plots surveyed for Kittlitz's murrelet nesting habitat characteristics on Kodiak Island, Alaska during 2008-2011. Outlined areas indicate convex hulls around each of the three habitat plot types: Nest = centered on a Kittlitz's murrelet nest; Near-nest = located at random near a Kittlitz's murrelet nest; Random = located at random within the area searched for Kittlitz's murrelet nests. PC 1 is characterized by strong positive loading for % vegetation cover and negative loading for rock size classes from < 1 cm up to 10-30 cm. PC 2 is characterized by moderate positive loading for rock size classes < 1 cm and 1-5 cm, and negative loading for rock size class 10-30 cm.

Table 3.3. Results of best-subset multiple logistic regression models incorporating ground cover covariates suggested by orthogonal principal component (PC) axes for plots centered on nests of Kittlitz's murrelets found on Kodiak Island, Alaska during 2008-2011. Nest plots are compared to plots near the nest and randomly selected plots within the nest search area. Parameter estimates represent log odds ratios relative to a one-increment change in each respective predictor.

Model	Predictor	Estimate	Std. error	*P*-value
Nest plots vs. random plots	Intercept	6.664	1.110	< 0.0001
	Ocean view (factor)	0.739	0.415	0.0753
	Slope	0.142	0.038	0.0002
	% Vegetation cover	-0.048	0.021	0.0187
	% Rock cover size 10–30 cm	0.053	0.016	0.0009
	% Rock cover size > 30 cm	-0.042	0.019	0.0246
Nest plots vs. near-nest plots	Intercept	4.740	1.333	0.0004
	Slope	0.137	0.046	0.0031
	% Vegetation cover	-0.047	0.023	0.0435
	% Rock cover size 10–30 cm	0.075	0.023	0.0010
	% Rock cover size > 30 cm	-0.057	0.024	0.0148
Near-nest plots vs. random plots	Intercept	2.682	0.532	<0.0001
	Slope	0.045	0.019	0.021

Table 3.4. Mean scaled conditional variable importance scores from random forest classifications for comparison of habitat characteristics of plots (1) centered on Kittlitz's murrelet nests, (2) centered on randomly selected points 50-150 m from a nest, and (3) centered on randomly selected points within the area surveyed for Kittlitz's murrelet nests on Kodiak Island, Alaska during 2008-2011. Conditional variable importance rank in parentheses. Bold values correspond to predictors selected in final logistic regression models.

Predictor	Nest vs. random	Nest vs. near-nest	Near-nest vs. random
% Rock 10–30 cm	**1.56 (1)**	**2.29 (1)**	-0.48 (11)
Slope	**1.51 (2)**	**0.29 (3)**	**1.42 (1)**
% Rock 5–10 cm	0.94 (3)	-0.02 (5)	-0.65 (12)
% Vegetation (25 m)	**-0.10 (4)**	**-0.01 (4)**	-0.46 (9)
Ocean view	**-0.23 (5)**	-0.51 (11)	0.43 (3)
% Rock > 30 cm	**-0.32 (6)**	**0.80 (2)**	0.30 (4)
Edge distance (m)	-0.48 (7)	-0.46 (8)	-0.46 (8)
% Rock 1-5 cm	-0.52 (8)	-0.54 (12)	1.19 (2)
% Rock < 1 cm	-0.54 (9)	-0.51 (10)	-0.38 (6)
% Orange crustose lichens	-0.57 (10)	-0.41 (6)	-0.46 (10)
Elevation (m)	-0.61 (11)	-0.46 (7)	0.00 (5)
% Lichen cover	-0.63 (12)	-0.47 (9)	-0.45 (7)

CHAPTER 4

SYNOPSIS AND CONCLUSIONS

Matthew James Lawonn

The aspects of Kittlitz's murrelet breeding ecology and nest site selection detailed in this thesis are consistent with the hypothesis that predation has been a significant selective force in the evolution of the species' breeding strategy. Kittlitz's murrelets nesting on Kodiak Island tended to visit their nests during crepuscular periods and made relatively few visits to the nest to provision chicks compared to other piscivorous, semi-precocial alcids. Kittlitz's murrelet chicks were almost exclusively provisioned high-lipid forage fish, grew rapidly, and had very short nestling periods. Nests experienced low survival rates in all study years, and predation appeared to be the most important cause of nest failure. Nest sites were in areas with little or no vegetation, both at the small (5 m) and intermediate (25 m, 50m) spatial scales, and were located farther from the edges of densely vegetated areas compared to randomly selected sites. All of these characteristics suggest that nest predation is a profoundly important selective force on the reproductive life history traits of Kittlitz's murrelet.

Until recently, knowledge about the breeding ecology of *Brachyramphus* murrelets has been limited relative to most other alcids, largely because of the extreme difficulty involved in locating and accessing nest sites. Through discovery of a large number of accessible Kittlitz's murrelet nests and use of relatively new nest monitoring technology, the research detailed in this thesis draws upon one of the more extensive and comprehensive datasets to date on the breeding ecology of any *Brachyramphus* species. Because all three species of *Brachyramphus* murrelets appear to share many attributes of their breeding ecology, I will discuss aspects of the breeding ecology of Kittlitz's

murrelet within the context of the genus as a whole, before discussing particular conclusions related to Kittlitz's murrelet.

The problem of predation has been mitigated for most alcid species by the selection of nesting habitats that are free of, or inaccessible to, terrestrial predators, and by adopting nesting strategies, such as burrow or crevice nesting, that discourage avian predators. The only alcids that nest in open, exposed, and unprotected sites besides *Brachyramphus* murrelets are the cliff-nesting murres, which, because of their large body size and nest guarding behaviors, are able to defend their eggs and chicks against many species of avian predators (Harris and Birkhead 1985). *Brachyramphus* murrelets, on the other hand, appear to rely solely on crypsis to avoid predation. In theory, there are distinct advantages to such a strategy. Crypsis allows parents to forego nest guarding during the chick-rearing stage, which frees both parents to forage at sea for themselves and for their growing chick. Besides increasing the chick meal delivery rate, such a strategy allows both parents to make a provisioning trip to the nest during the same crepuscular period, when predation risk is presumably minimized. Moreover, relief from nest guarding duty, as well as the very short chick-brooding period for *Brachyramphus* murrelets, would have energetic benefits for adults because they would be able to allocate time toward feeding that would otherwise be spent at the nest site. Such energy savings may allow adults to select nest sites at greater distances from foraging areas and the coast, because adults would have sufficient energy reserves to make possible long-distance provisioning flights to the nest. Cryptic, non-colonial breeding may also increase

the total area available for nesting. While all other alcids are largely restricted to a limited number of predator-free island habitats for breeding, and must deal with potential depletion of food resources around colony sites (Ashmole 1963, Birt et al. 1987), the generally mainland-nesting *Brachyramphus* murrelets may have increased flexibility to select nest sites in relative close proximity to quality foraging areas that are underexploited by other pursuit-diving seabirds. Foraging in such areas would be precluded for colonial-nesting species if suitable nesting habitats were not available within an energetically feasible commuting distance.

There are, however, serious trade-offs for nesting cryptically and non-colonially. The first is extreme sensitivity to increased predation pressure. The efficacy of crypsis as a nesting strategy is highest when the potential encounter rate with predators is low (Merilaita et al. 1999). Fluctuations in predator densities, and thus encounter rates, would be expected to have profound implications on nesting success for *Brachyramphus* murrelets because nests are essentially indefensible to predator attack. Nests of other alcid species, especially those that nest in burrows or crevices, would be somewhat resistant to increased predator numbers because the efficacy of their anti-predator strategies is more or less independent of predator encounter rates, at least in the case of avian predators. Additionally, mainland breeding habitats may put adult murrelets at higher risk from avian predators compared to offshore colony sites. Owing to high wing-loading, alcids in general are not very maneuverable in flight, and their best defense in the face of avian attack is often to dive (Lima 1993). *Brachyramphus* murrelets flying

over mainland habitats essentially have no defense against avian attack with the exception of their considerable speed, but numbers of adult Kittlitz's murrelets taken by peregrine falcons (*Falco peregrinus*) and bald eagles (*Haliaeetus leucocephalus*) near Icy Bay (Kissling 2007) suggest that this may not be an effective defense against some avian predators.

Another potential drawback to the *Brachyramphus* murrelet strategy of using dispersed and cryptic nest sites, and their breeding ecology in general, is an apparent high reliance on high-lipid schooling forage fish as a food source for developing chicks (Burkett 1995, Nelson 1997, this study). Schooling forage fish are generally considered to be less predictable in time and space than low-lipid, non-schooling demersal fishes (Cairns 1987, Litzow et al. 2004a, 2004b). While the piscivorous, offshore-foraging alcids also rely heavily on such unpredictable schooling species, they may be more resistant to the effects of poor foraging conditions related to the unpredictability of prey compared to *Brachyramphus* murrelets. This is because the chick growth rates of offshore-foraging alcids are generally low; hence, peak food demand for chicks is lower. Longer nestling periods that accompany relatively slow growth would not necessarily result in increased predation risk for offshore-foraging alcids, because their nests are either defended or relatively secure from predators.

For *Brachyramphus* murrelets, a longer nestling period translates into a longer period of exposure to predation, and necessarily entails a higher predation risk. Also, there is evidence that the coloniality of offshore-breeding alcids is itself an adaptation to

effectively exploit unpredictable prey resources (Ward and Zahavi 1973, Harris and Birkhead 1985). Colony members can efficiently maximize their own provisioning success by focusing their foraging efforts on areas where their colony-mates have successfully foraged. Additionally, large groups of foraging seabirds that often occur near colony sites probably serve as effective signals for the location of concentrated prey (Davoren et al. 2003), although competition for these resources may depress foraging success rates.

Seabird species that nest solitarily are not able to learn the locations of quality foraging areas from conspecifics as easily as colonial species, and hence may be at an inherent disadvantage in locating prey that are unpredictable in space and time. It would be expected, therefore, that the costs of locating prey might be higher for the non-colonial *Brachyramphus* murrelets, than for colonial species of alcids. On the other hand, once prey are located, prey availability may be greater than in offshore situations, because competition is presumably limited due to the absence of a colony effect.

The reasons that *Brachyramphus* murrelets appear to favor relatively unpredictable, but high-quality prey may relate to an interaction between commuting distance from foraging areas to nest sites and predation risk. The relatively poor quality of predictable, low-lipid prey does not appear to be a factor in itself, as is illustrated by the success of the pigeon guillemot (*Cepphus columba*) in utilizing such prey during reproduction. The pigeon guillemot occupies a similar inshore foraging niche as *Brachyramphus* murrelets, but its breeding ecology is radically different. It makes large

numbers of daily deliveries (0.7–1.9 fish/h, Ewins 1993) to relatively safe nest sites typically situated in crevices in areas free of terrestrial predators. Nest sites are typically close to foraging grounds, where adults capture primarily predictable, low-lipid demersal fishes to provision their brood, which frequently consists of two chicks.

The benefits of such a strategy appear to be great: chick growth in pigeon guillemots is among the highest of semi-precocial alcids and chicks typically fledge at approximately adult body mass (Gaston and Jones 1998). However, I posit that such a strategy of exploiting predictable, but low-quality demersal fishes is a poor option for *Brachyramphus* murrelets for three reasons. First, making chick-provisioning trips to the nest at a high rate is only a tenable strategy when the probability of nest predation is relatively unrelated to the number of provisioning trips. Such would not be the case for cryptic nesters, such as *Brachyramphus* murrelets, because movement near the nest site related to chick provisioning would presumably elevate the risk of detection by a predator. Second, the distance between nest sites and foraging areas appears to be greater for *Brachyramphus* murrelets than the pigeon guillemot (Gaston and Jones 1998). Flight costs appear to comprise the largest portion of the energy budgets of breeding Kittlitz's murrelets (Hatch 2011), and relatively long commuting distances may make provisioning large numbers of low-lipid forage fish energetically unprofitable for *Brachyramphus* murrelets. Finally, evidence suggests that the risk of avian predation for provisioning adults may be high for *Brachyramphus* murrelets (Whitworth et al. 2000, Kissling 2007); this risk may preclude a strategy that involves large numbers of deliveries because the

cumulative mortality risk to adults may be expected to be proportional to the number of deliveries required to fledge a chick.

By provisioning high-lipid prey, *Brachyramphus* murrelets are able to deliver large amounts of energy to rapidly growing chicks while minimizing the number of provisioning flights necessary. This has the added benefit of allowing flexibility in the timing of food deliveries. *Brachyramphus* murrelets are able to make a large proportion of meal deliveries during crepuscular time periods when predation risk is presumably minimized because relatively few fish are needed to meet the energy requirements of growing chicks.

Based on the previous discussion, it follows that ideal conditions for breeding in *Brachyramphus* murrelets occur when predator encounter rates are very low at both the nest site and for adults commuting to the nest site, where nest sites are situated close to good foraging areas, and where high-quality forage fish are predictably available. Such ideal foraging areas would also be relatively unexploited by other pursuit-diving seabirds. For Kittlitz's murrelets, such conditions exist where terrestrial habitats characterized by glacial activity lie in close proximity to coastal areas. Suitable rocky slopes for nesting are created by glacial recession, and steep slopes carved by former glaciers may remain vegetation-free if sufficiently unstable or at high elevations. These vegetation-free habitats are abundant, and are often situated very close to potential foraging areas in many core areas of the Kittlitz's murrelet's range (USFWS 2011). Because extensive scree slopes suitable for nesting occur within large expanses of rugged, un-vegetated

terrain, numbers of terrestrial predators are probably extremely low, and avian predators are likely also rare near nest sites.

The abundance of potential forage appears to be very high near areas of significant glacial outflow (Arimitsu et al. 2004, 2008, 2012). High densities of euphausiids are found at the termini of tidewater glaciers and in fjords with glacial outflow, and schooling forage fish appear to be present in high numbers in such areas as well, especially in mid to late-summer, when most chick provisioning occurs (Arimitsu et al. 2012). Paradoxically, typically unpredictable forage fish species, such as capelin, Pacific sand lance, and juvenile herring, may be quite predictable and abundant in the "milky" waters of glacial outflow, allowing for the non-colonial nesting Kittlitz's murrelet to find forage fish without benefit of the information-sharing that is characteristic of colonial species. Moreover, the moderate turbidity of such water appears to concentrate forage species near the surface, where light is sufficient for primary production, and where they are relatively accessible to foraging seabirds (Arimitsu et al. 2012). The large eye size of Kittlitz's murrelet is thought to be an adaptation for effective foraging in such turbid waters (Day et al. 2003).

While nesting near heavily glaciated areas appears to confer many benefits to Kittlitz's murrelets, the limited number and extent of these areas may constrain the total population of the species. Additionally, the influence of glacial recession on Kittlitz's murrelet breeding ecology may be significant. Most tidewater glaciers within the North American portion of the species' breeding range are currently receding (Arendt et al.

2002; reviewed in USFWS 2011), and while the future rate and extent of glacial recession is unclear, these changes may translate into changes in the suitability of habitats for breeding by Kittlitz's murrelets. Over the short term, glacial recession would be expected to increase the overall area of available habitat for nesting, as suitable vegetation-free substrates are exposed from beneath glacial ice. However, non-vegetated substrates, especially at low elevations, can be quickly colonized by pioneer plant communities following glacial recession (Matthews 1992), and thus may rapidly become unsuitable for nesting. The overall effect of glacial recession on available nesting habitat is, consequently, a complex and dynamic shift that involves simultaneous habitat creation and loss, complicating predictions of habitat change.

The quality of non-vegetated habitats may be expected to change coincident with glacial recession as well. While the total area available to nesting Kittlitz's murrelets may increase over the short term, primary plant succession on a broad scale may make non-vegetated areas increasingly fragmented and more accessible to predators, and increasingly prone to deleterious edge effects related to predation. My thesis research revealed that Kittlitz's murrelet nests were situated farther from edges of densely vegetated areas than randomly selected sites, which may reflect a tendency of the species to prefer nest sites in the interior of large patches of non-vegetated habitat. Additionally, habitats within my study area were relatively fragmented and had a high proportion of edge, because sparsely-vegetated habitats were irregularly shaped and dissected by strips of vegetation. It is possible that the very high depredation rates that I observed in my

study were related to the proximity of vegetated edges to all suitable nesting habitat for Kittlitz's murrelets. The possible benefit of glacial recession over the short-term, therefore, could be offset in the long-term by higher nest depredation rates related to decreasing patch size and enhanced edge effects.

The effects of glacial recession on foraging conditions for Kittlitz's murrelets are likewise unclear. Kittlitz's murrelets appear to be strongly associated with bays and fjords that are heavily affected by tidewater glaciers (Kendall and Agler 1998, Day et al. 2000, Kuletz et al. 2003), and there is some evidence that they prefer to forage near advancing or stable tidewater glaciers, rather than near receding glaciers (Kuletz et al. 2003). Potential reasons for avoidance of areas with receding glaciers include depressed numbers of invertebrates, primarily euphausiids, and forage fish associated with extremely turbid water from high rates of glacial ablation, and possibly poorer foraging efficiency by Kittlitz's murrelets, also associated with extreme turbidity (Kuletz et al. 2003). If glacial recession results in a reduction in the number of active tidewater glaciers near nesting habitats, Kittlitz's murrelet may experience reduced foraging efficiency in the same habitats where new nesting habitat is being created. Hence, although suitable nesting habitat may be created by rapid glacial recession, a decline in the quality of nearby foraging habitat may make such areas poor choices for potential nesters.

The importance of nesting terrain that is not influenced by glacial activity for the global population of Kittlitz's murrelets is unknown. The studies presented in this thesis were conducted in terrain far from tidewater glaciers, although areas of significant glacial

outflow were approximately 70 km from the study area, apparently within the potential commuting distance for incubating and provisioning adults (Day et al. 1999). Nests unassociated with glaciers have been found in the Aleutian Islands and north of the Alaska Peninsula along the Bering and Chukchi seas, indicating that a significant number of Kittlitz's murrelet may breed in areas without glaciers (Day et al. 1999, Kaler et al. 2009). Given the results of my thesis, I would predict that other areas with a combination of mountainous habitats, few terrestrial predators, and rich forage fish resources would also be suitable Kittlitz's murrelet breeding habitat.

RECOMMENDATIONS FOR FURTHER RESEARCH

The results of this thesis suggest a fundamental hypothesis: the breeding ecology of the Kittlitz's murrelet represents a trade-off between low daily nest survival and high adult predation risk (relative to non-*Brachyramphus* alcids) vs. the benefits of rich foraging opportunities made available by such a nesting strategy. This hypothesis suggests several testable predictions that could be addressed in future research:

1) Reproductive success of Kittlitz's murrelets will be highly sensitive to changes in predation pressure and the availability/quality of forage fish resources, and will be highest in habitats with few predators and where high-quality forage fish are relatively available and predictable in close proximity to nest sites.

2) In cases where the daily nest survival rate is high, the risk of predation on adults visiting nests is low, and commuting distances are short, Kittlitz's murrelets will be able to fledge young even when the quality of forage fish is relatively low (e.g., non-

schooling, low-lipid demersal fishes) because there would be little fitness penalty related to making large numbers of chick meal deliveries over an extended nestling period.

3) In areas with low nest survival rates and high predation risk for parents, predictable, high-quality forage fish resources are necessary to ensure high chick growth rates and relatively few chick provisioning visits. Under these conditions, declines in prey quality or foraging success would not only negatively affect chick growth rates and cause longer nestling periods, but would also reduce both nest and adult survival rates.

4) The limits on the distance of nests from at-sea foraging areas are positively related to forage fish quality. When forage fish are predictable, available, and high-quality, nest sites can be located a great distance from foraging grounds because reproductive investment (i.e., energetic cost and predation risk) is lower than when forage fish are sparse, unpredictable, and low-quality. Hence, the effective area of suitable nesting habitat is greatest for Kittlitz's murrelets when forage fish resources are relatively predictable, available, and high-quality, and lowest when forage fish resources are unpredictable, sparse, and low-quality, or if prey become difficult to capture.

The apparent poor reproductive success of Kittlitz's murrelets on Kodiak Island (this thesis) and elsewhere in Alaska (USFWS 2011) is cause for concern.
An expanded monitoring effort is needed to determine whether the low nest success rates encountered during this study are representative across the species range and whether they reflect a long term trend. A continued monitoring effort on Kodiak Island is needed to determine long-term trends for Kittlitz's murrelet reproductive success within the

study area described in this thesis. Evaluation of occupancy and nest success rates in higher elevation areas on Kodiak Island would help determine whether differences in nest survival, predation rates on nests, and nest site selection exist among nesting areas with different habitat characteristics.

Trends in potential Kittlitz's murrelet predators are unclear, both on Kodiak Island, and in other potential nesting areas in Alaska. Given the apparent sensitivity of the species to predation, long term population monitoring of likely predators including red fox, common raven (*Corvus corax*) bald eagles, and peregrine falcons is necessary to determine whether changes in predator densities is a plausible explanation for apparent population declines.

A large proportion of the global population of Kittlitz's murrelets appears to breed in areas dominated by glaciated landscapes and tidewater glaciers. Future research that explores the potential effects of climate change on the area and quality of nesting habitat, on the availability of high-quality forage fishes, and on potential predators of nests and adults will be crucial for determining the long-term availability and quality of breeding sites in these areas. My thesis research suggests that Kittlitz's murrelets are able to support high chick growth rates in areas far from glaciated coastlines. More research is needed to elucidate the foraging ecology of Kittlitz's murrelets in these areas to better understand how the species may respond to potential changes in foraging conditions in areas characterized by glacial recession. Finally, the discovery of apparent significant chick mortality as a result of parasitic infection and saxitoxin exposure suggests that

these factors could significantly constrain reproductive output, and clearly warrant further research.

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